Hydrology and Biogeochemistry of Tropical Montane Rain Forests of Contrasting Stature in the Blue Mountains, Jamaica

Hafkenscheid, R.L.L.J.

2000

Hydrology and biogeochemistry of tropical montane rain forests of contrasting stature in the Blue Mountains, Jamaica

Raimond Hafkenscheid

Hydrology and biogeochemistry of tropical montane rainforests of contrasting stature in the Blue Mountains, Jamaica

Raimond L. L. J. Hafkenscheid

Front cover : early morning clouds over John Crow Peak. Photo taken from Bellevue towards the west.

Back cover : a selection of photographs of the fieldwork in Jamaica.
Photo at the left top corner by Erik Veneklaas.
All other photos by Raimond Hafkenscheid.

Printed by: Print Partners Ipskamp, Enschede, The Netherlands

VRIJE UNIVERSITEIT

Hydrology and Biogeochemistry of Tropical Montane Rain Forests of Contrasting Stature in the Blue Mountains, Jamaica

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor aan
de Vrije Universiteit te Amsterdam,
op gezag van de rector magnificus
prof.dr. T. Sminia,
in het openbaar te verdedigen
ten overstaan van de promotiecommissie
van de faculteit der aardwetenschappen
op donderdag 11 mei 2000 om 15.45 uur
in het hoofdgebouw van de universiteit,
De Boelelaan 1105

door

Raimond Lodewijk Leonardus Johannes Hafkenscheid

geboren te 's-Gravenhage

Promotor : prof.dr. I. Simmers
Copromotoren : dr. L.A. Bruijnzeel
: dr. H.A. Verhoef

This study was financed by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) under grant no. W76-371 and through a donation by the Dr Jacoba Ruinen Foundation for Canopy Research.

CONTENTS

List of Figures

List of Tables

1

GENERAL INTRODUCTION

1.1 INTRODUCTION

As one ascends wet tropical mountains, marked changes in forest structure and physiognomy occur, notably a decrease in stature and average leaf size with increasing elevation, whereas the leaves tend to become thicker and harder as well [*Grubb*, 1977]. In addition, the 'mossiness' of the forest increases with elevation [*Frahm and Gradstein*, 1991]. When characterizing the vegetation on wet tropical mountains, a distinction is often made between relatively tall-statured 'lower montane rain forest' (LMRF) and smaller-statured 'upper montane rain forest' (UMRF) which is generally situated directly above the LMRF belt [*Grubb et al.*, 1963]. This subdivision of montane forest types has been related to the presence of fog and low cloud by *Grubb and Whitmore* [1966] who suggested that LMRF had 'frequent' and UMRF 'long persistent' cloud cover close to the ground. Later, *Grubb* [1974] stated that tall LMRF could also occur in places that are largely free of fog. Although quantitative criteria of what constitutes 'frequent' or 'long persistent' fog are lacking in the definitions of *Grubb and Whitmore* [1966], their altitudinal classification of forest types is supported by numerous descriptive studies and bryophyte surveys [*Richards*, 1952; *Van Steenis*, 1961; *Stadtmüller*, 1987; *Proctor et al.*, 1988; *Frahm and Gradstein*, 1991].

More than 35 different names have been proposed to describe tropical montane forest environments and appearances in various languages but the simplifying term 'montane cloud forest' has been coined to denote any montane forest subject to 'frequent fog incidence' [*Stadtmüller*, 1987]. As such, a 'typical' or 'true' cloud forest is most likely to belong to the UMRF type of *Grubb and Whitmore* [1966], although LMRF subject to intermittent cloud incidence may also classify as cloud forest [*Kitayama* [1995] and references therein]. Although it lacks quantification, the term 'cloud forest' reflects the general recognition that cloud incidence exerts a dominant influence on a range of forest hydrological and ecological processes (see also the next section).

Montane cloud forests are distributed throughout the tropics and cover a large altitudinal range. They were estimated to occupy *c.* 500,000 km^2 in the early seventies [*Persson*, 1974] but have since been disturbed and reduced at an alarming rate [*Henderson et al.*, 1991; *Hamilton et al.*, 1995]. On large equatorial mountains, the lower boundary of montane cloud forests is generally found between 1500 and 2500 m a.s.l., whereas its upper boundary has been reported between 2400 and 3300 m a.s.l., depending on prevailing temperatures

and atmospheric humidity (but not rainfall) [*Lauer*, 1986; *Stadtmüller*, 1987].

Away from the equator, the position of vegetation belts tends to decrease in elevation with increasing latitude, presumably reflecting the gradual reduction in mean temperatures [*Troll*, 1948; *Ohsawa*, 1995]. However, on small coastal mountains in the humid tropics, low-statured mossy forest may occur at much lower elevations (300–1000 *m* a.s.l.) than on similar-sized or larger mountains situated more inland. This phenomenon, in which the vegetation zonation on small mountains is compressed, is often referred to as the 'Massenerhebung' (mass elevation) effect [*Richards*, 1952] or the 'telescoping' effect [*Van Steenis*, 1972]. Originally [*Schröter*, 1926], the 'Massenerhebung' effect was based on the idea that the larger heat storage capacity of large mountain massifs could raise ambient air temperature and therefore extend vegetation zones in a upward direction. The fact however that the compression of vegetation zonation is rarely observed in the seasonally dry tropics [*Van Steenis*, 1972] and becomes less pronounced on mountains located more inland, suggests an atmospheric humidity aspect as well. *Bush* [1986] referred to this as the 'coastal proximity effect' (see also below).

1.2 Forest stunting on wet tropical mountains

In comparison with lower altitude tropical rain forests, montane cloud forests are generally characterized by a reduction in tree stature, stem diameter and the number of individual trees per unit area, as well as by an increase in stem density (*i.e.* an increase in the number of multiple-stemmed trees). Canopy trees often show gnarled trunks and branches and the leaves tend to be smaller, thicker and harder (more sclerophyllous) [*Whitmore*, 1998]. On the other hand, the biomass of epiphytes on stems and branches is higher [*Frahm and Gradstein*, 1991], with a corresponding reduction in woody climbers. Whilst the number of tree species in cloud forest is reduced compared to lowland forests, the diversity of shrubs, herbs and epiphytes, as well as the number of endemics per unit area, are generally high [*Gentry and Dobson*, 1987; *Hamilton et al.*, 1995; *McKinnon et al.*, 1996].

The reduced tree stature of certain montane cloud forests, notably those situated on and around ridge- and mountain tops, is often referred to as 'forest stunting'. Both forest stunting and the occurrence of low-statured mossy forest at low elevations on small humid tropical mountains have been studied intensively (see reviews by *Leigh* [1975], *Grubb* [1977, 1989], *Stadtmüller* [1987], *Tanner et al.* [1998], *Bruijnzeel and Veneklaas* [1998]). Yet, the two phenomena have remained largely unexplained. As related earlier, *Grubb and Whitmore* [1966] suggested that the frequency of occurrence of fog (low cloud) is the single most important factor determining the stature of montane forest. Although the associated actual mechanisms are only partially understood, a number of variables and processes are evidently influenced by the occurrence of fog:

- The presence of fog and low cloud may reduce irradiance by 10–50 %

compared to conditions outside the cloud belt [*Baynton*, 1968; *Aylett*, 1985; *Cavelier and Mejia*, 1990; *Bruijnzeel et al.*, 1993]. Also, the rapid fluctuations in the density of the passing fog will create frequent short-term fluctuations in solar radiation that may influence leaf physiology [*Cavelier*, 1988].

- Reduced insolation and air temperature and increased humidity will lead to a considerable reduction in evaporative demand and may hamper transpiration in extreme cases [*Weaver et al.*, 1973; *Ash*, 1987].

- Fog not only represents an extra hydrological input ('horizontal' or 'occult' precipitation; *Zadroga* [1981]) but will also extend the period during which the canopy is wet and transpiration is halted [*Rutter*, 1975]. In addition, persistent leaf wetness may induce a chronic reduction of photosynthesis in some plants [*Ishibashi and Terashima*, 1995].

- The strongly altered water balance in the cloud-affected zone may cause soils to be persistently wet, thus influencing litter decomposition, soil acidity, aluminium and aeration levels, as well as root development and functioning [*Wadsworth and Bonnet*, 1951; *Hetsch and Hoheisel*, 1976; *Steinhardt*, 1979; *Jane and Green*, 1985; *Silver et al.*, 1999].

- The high acidity and nutrient content of fog water compared to rain [*Asbury et al.*, 1994] may affect leaf physiology and nutrient relations [*Schier and Jensen*, 1992].

Over the years, numerous hypotheses have been advanced to explain the occurrence of stunted forest and the compressed zonation of vegetation on wet tropical mountains (recently reviewed by *Bruijnzeel et al.* [1993] and *Bruijnzeel and Veneklaas* [1998]). Many of these hypotheses are closely interrelated to one another, making it difficult to distinguish 'causes' and 'consequences'. Given the high degree of uncertainty surrounding the cumulative effects of interrelated processes, it is not surprising to find that several hypotheses and findings of different studies have contradicted one another. This was recognized by *Whitmore* [1989], who rejected the idea of a single uniform set of explanations, and by *Weaver et al.* [1986], who referred to a possible cumulative effect of multiple stress factors. In a more general review of montane forest productivity, *Bruijnzeel and Veneklaas* [1998] drew particular attention to the scarcity of information on the overall carbon economy of tropical montane forests and the influence of climate and soil conditions thereupon. In the following the most important hypotheses on the causes of forest stunting on wet tropical mountains are briefly discussed.

Soil saturation and impeded root respiration
Soil saturation or persistently wet soils will have a major impact on aeration levels [*Silver and Vogt*, 1993; *Silver et al.*, 1999] and the respiration ability of roots [*Jane and Green*, 1985] which would limit reproduction of fine roots and

nutrient uptake capacity and thus, ultimately, forest stature. Many studies (but not all) have reported persistent (near-) saturated conditions in montane cloud forest soils [*Wadsworth and Bonnet*, 1951; *Lyford*, 1969; *Herrmann*, 1971; *Hetsch and Hoheisel*, 1976; *Dohrenwend*, 1979; *Jane and Green*, 1985; *Bruijnzeel et al.*, 1993], presumably as a result of additional horizontal precipitation inputs and low evaporation [*Bruijnzeel and Proctor*, 1995]. However, on Rakata, Indonesia, stunted forest occurs on highly permeable young volcanic soils that lack any hydromorphic features. It is virtually certain that these soils never become water logged [*Hafkenscheid*, 1994]. *Kapos and Tanner* [1985] also reported that it is highly unlikely that the soils below several stunted ridge top forests in Jamaica were ever to become completely saturated. It must therefore be concluded that excessive waterlogging cannot be ruled out as a potential cause of the occurrence of stunted forest in many places but that such forest can also occur on well-drained soils.

Periodic water shortage
Trees growing in upper montane cloud forests on shallow soils have been reported to die following severe droughts [*Lowry et al.*, 1973; *Werner*, 1988]. On the other hand, most observations of soil water dynamics and leaf water potentials in cloud forest have reported wet to very wet soil conditions (see previous paragraph) with little chance that the trees would ever suffer severe water stress. However, plants adapted to sustained high soil moisture levels may be more sensitive to prolonged dry spells because of their poorly developed root system [*Jane and Green*, 1985]. Unfortunately, soil water observations that lasted long enough to include rare droughts are lacking, which makes it difficult to assess the impact of drought on montane forest stature. However, low sensitivity to drought by montane cloud forests in East Malaysia was demonstrated by *Bruijnzeel et al.* [1993]. Here, an exceptional drought did not affect the vegetation within the cloud zone whereas forests at lower altitudes showed a significant increase in leaf shedding. It is most likely, therefore, that drought stress will only play a role in areas with shallow soils of low water holding capacity [*Van Steenis*, 1972].

Reduced air and leaf temperatures
It has been suggested that low forest stature on tropical mountains could be caused by reduced leaf temperatures associated with reduced radiation inputs [*Grubb*, 1977]. Although data on leaf temperatures in tropical montane forests are rare, *Kapos and Tanner* [1985] showed that differences between leaf and air temperatures were very small. As such, it is hard to imagine that the temperatures of leaves in stunted forests at low elevations will be so low as to adversely affect the balance between photosynthesis and respiration. Cooling by transpiration plays an important role in the leaf energy budget [*Gates*, 1969] but all available evidence on transpiration in short-statured forests suggests this to be very low [*Bruijnzeel and Proctor*, 1995]. This should lead to higher rather than lower leaf temperatures [*Medina et al.*, 1978]. Transpiration is strongly governed by canopy conductance which, in turn, is mainly a function of leaf

area index (LAI) and stomatal conductance. LAI of tropical montane forest ranges from *c.* 6 in LMRF with little low cloud [*Grubb*, 1977] to *c.* 2 in dwarf cloud forest [*Weaver et al.*, 1986]. Stomatal sizes and densities in cloud forests are not lower compared to lowland forests [*Cintron*, 1970; *Grubb*, 1977; *Tanner and Kapos*, 1982] whereas measured stomatal conductance covers a wide range [*Bruijnzeel and Veneklaas*, 1998]. It seems therefore that stomatal conductance in montane cloud forest is not inherently low but that stomatal behaviour is such that conductance is often reduced and transpiration accordingly low [*Bruijnzeel and Veneklaas*, 1998]. The observation that LAIs in cloud forests are relatively low may indicate that further expansion of leaf area would only lead to leaves that function below their light compensation point.

Various studies have suggested that levels of photosynthetically active radiation (PAR) in cloud forests remain above light saturation levels required for photo-assimilation [*Aylett*, 1985; *Turton*, 1990; *Hafkenscheid*, 1994]. However, in a simulation exercise of carbon gains of a cloud forest canopy with specified photosynthetic characteristics as a function of LAI for the two hypothetical extreme cases of permanently sunny or overcast conditions, *Bruijnzeel and Veneklaas* [1998] showed that during fully clouded conditions, carbon gain at the top of the canopy was lower and the rate of decrease with depth in the canopy faster. The integrated carbon gain of the total canopy increased with cumulative LAI up to the point where additional leaves respired more than they assimilated. Under fully overcast conditions this point was reached for an LAI of *c.* 2 *vs.* an LAI of 4–5 under sunny conditions. Such simulations support the idea that irradiance levels constitute a key controlling factor although the precise mechanisms require more study [*Bruijnzeel and Veneklaas*, 1998].

Nutrient limitation

Limited nutrient supply has been considered an important potential explanation of montane forest stunting in many cases [*Tanner et al.*, 1998]. This may be related to extreme acidity of peaty topsoils that could hamper uptake of key nutrients [*Tanner*, 1977b], induce aluminium toxicity [*Northup et al.*, 1995], overall low fertility of the substrate [*Van Steenis*, 1972], or reduced decomposition and mineralization rates [*Grubb*, 1977; *Marrs et al.*, 1988]. However, no generalizations about the soil chemistry of montane forests are free of exceptions [*Bruijnzeel and Proctor*, 1995]. Stunted montane forest has been found at low elevations on soils with pH values of 6.4–6.8 [*Cavelier*, 1988; *Hafkenscheid*, 1994]. Therefore, low soil pH (or associated aluminium toxicity) cannot be held responsible in general for the occurrence of stunted forest. Similarly, exchangeable bases and percentage base saturation are usually low in montane soils, but not invariably so [*Bruijnzeel and Proctor*, 1995].

Although nitrogen mineralization and nitrification rates have been found to decline with elevation in response to increased soil wetness on some mountains [*Marrs et al.*, 1988], rates in various stunted montane forests were relatively high [*Tanner*, 1977b; *Hafkenscheid*, 1994]. Nutrient concentrations in litterfall in montane forests are variable, but a distinct trend to lower nitrogen (but not phosphorus) concentrations with elevation can be observed in those cases

where measurements have been made at different elevations on the same mountain [*Bruijnzeel and Proctor*, 1995]. However, when comparisons are made between element concentrations in fresh foliage and litterfall, proportionally more translocation is indicated of phosphorus than nitrogen before leaf abscission. Such observations on litterfall nutrients seem in general agreement with the idea supported by (heavy) fertilization experiments that nitrogen, or nitrogen *and* phosphorus, may limit the growth of some tree species in cloud forests [*Tanner et al.*, 1998].

However, *Bruijnzeel* [1989a] and *Bruijnzeel et al.* [1993] showed that nutrient inputs via (net) precipitation greatly exceeded the corresponding amounts immobilized in the above-ground biomass of low-statured montane forests in Jamaica and East Malaysia, respectively. This would suggest that tree nutrient uptake ability rather than the availability of nutrients *per se* is the key factor. *Grubb* [1977] already dismissed the hypothesis that nutrient uptake rates in montane forests were climatically reduced to critically low levels [*Odum*, 1970; *Ash*, 1987]. [*Bruijnzeel et al.*, 1993] suggested an interference with nutrient uptake by phenolic substances (see below).

Phenolic metabolites

An important role in the unraveling of the Gordian knot of interrelated 'forest stunting' hypotheses may be reserved for phenolic metabolites. Originally presented as a major factor in herbivory control [*Janzen*, 1974], increased concentrations of phenols in plant tissue are now known to be the result of various stress factors, notably water or nutrient deficiencies [*Horner et al.*, 1988], high irradiance (including UV-B) levels [*Levitt*, 1980; *Ziska et al.*, 1992], or high soil acidity and associated aluminium toxicity [*Coulson et al.*, 1960; *Muller et al.*, 1987; *Nicolai*, 1988; *Northup et al.*, 1995]. In turn, polyphenols have been reported to affect photosynthesis [*Einhellig et al.*, 1970; *Patterson*, 1981; *Kuiters and Sarink*, 1987], cell division in fine roots [*Vaughan and Ord*, 1990], nutrient uptake [*Glass*, 1973, 1974; *Kobza and Einhellig*, 1987; *Kuiters and Sarink*, 1987] and stomatal control [*Einhellig and Kuan*, 1971]. Moreover, polyphenols and cell proteins in foliage may form complexes during leaf senescence which may result in litter that is recalcitrant to decomposition, an accumulation of humus and a reduction in nutrient cycling efficiency [*Coulson et al.*, 1960]. *Northup et al.* [1995] suggested that complexation by polyphenols could reduce nutrient depletion by leaching in general and the loss of mobile nitrogen in particular. Polyphenols interacting with clay minerals and soluble aluminium in acid soils might also decrease the fixation of phosphorus, and thus increase phosphate availability and reduce aluminium toxicity [*Northup et al.*, 1995] although this remains to be demonstrated.

Concentrations of polyphenols in fresh leaf litter from cloud forests were found to be much higher compared to litter from forests below the cloud cap on several mountains in South-east Asia [*Bruijnzeel et al.*, 1993]. Because the concentrations in fresh material were much higher than in older litter, *Bruijnzeel et al.* [1993] hypothesized that the polyphenols had been washed into the soil where they could interfere with a range of ecological processes

along the lines described above. *Bruijnzeel and Veneklaas* [1998] concluded that further work is required to test the role and causes of enhanced phenol concentrations in montane cloud forests.

Strong winds
Exposure to high wind speeds has also been put forward as a cause for montane forest stunting [*Jaffe*, 1980; *Lawton*, 1982; *Sugden*, 1986]. Although it is clear that in some exposed locations within the trade wind belts strong wind do actually affect forest stature via wind pruning [*Sugden*, 1986], winds at equatorial latitudes rarely play a significant role [*Proctor et al.*, 1988; *Hafkenscheid*, 1994; *Pendry and Proctor*, 1996b]. According to *Bruijnzeel and Veneklaas* [1998], strong winds can therefore be rejected as a general explanation for forest stunting on low mountains in the humid tropics. However, winds may have an indirect effect as more moisture-laden air passing through the forest canopy would generate an increase in horizontal precipitation, and canopy wetting, and so reduce transpiration [*cf. Rutter*, 1975].

1.3 History of the present project

In an attempt to contribute to the remaining questions and uncertainties related to the development of small-statured forests and compressed zonation of vegetation on wet tropical mountains, researchers from the Vrije Universiteit Amsterdam (VUA) joined a series of mainly British-led expeditions between 1986 and 1993. Examples include expeditions to Mount Bloomfield (Philippines) in 1986 and 1987 [*Proctor et al.*, 1997, 2000a, b], Mount Silam (Malaysia) in 1987 and 1989 [*Bruijnzeel et al.*, 1993] and Gunung Rakata (Indonesia) in 1992 and 1993 [*Hafkenscheid*, 1994].

Whilst these short-term expeditions generated important information and new ideas (*inter alia* the potential importance of polyphenols), the respective sites either suffered from contrasts in floristic composition between forests within and below the cloud zone (which rendered any comparisons less than straightforward) or they were so remote as to become unsuitable for longer-term hydrometeorological and forest ecological process observations.

Grubb and Tanner [1976] and *Tanner* [1977a, b] described a series of montane ridge-top forests of contrasting stature and physiognomy located at *c.* 1550 *m* a.s.l. in the Blue Mountains of Jamaica. Situated on comparable geological substrates and experiencing similar climatological conditions, these forests show considerable overlap in floristic composition, making them particularly suited for the study of the causes of forest stunting. Earlier work by E. V. J. Tanner and co-workers in these forests has documented their basic characteristics (floristics, structure, biomass, foliar anatomy and nutrient contents), [*Tanner*, 1977a, b, 1980b, 1985; *Tanner and Kapos*, 1982] plus a range of forest ecological processes (litterfall, decomposition, nitrogen mineralization, physiology), [*Tanner*, 1977a, 1980a, 1981; *Kapos and Tanner*, 1985; *Aylett*, 1985]. Later work includes a series of bioassays and forest fertilization experiments [*Healey*, 1989;

Tanner et al., 1990] and a study of the ecological effects of forest disturbance by hurricanes [*Bellingham*, 1993] and landsliding [*Dalling*, 1992]. Needless to say, the existing database for these montane forests, together with the logistic possibilities provided by the nearby Botanical Gardens at Cinchona and the University of the West Indies (UWI) at Kingston rendered this area ideal for complementary studies and the testing of new hypotheses. Because it was realised from the outset that a combined hydrometeorological, pedological and ecological approach was likely to produce more meaningful results than individual mono-disciplinary efforts, a collaborative project was formulated involving contributions from specialists in each of these fields [*Bruijnzeel and Verhoef*, 1994].

The present project started in 1994 when funding was granted by the Netherlands Foundation for Advancement of Tropical Research (WOTRO; project no. W84–371) for research in the Cinchona area over a period of 4 years. In November 1994, the author moved to Jamaica to embark on an 18-month fieldwork period. Most of the field observations were conducted in two nearly adjacent forest plots of contrasting stature near Bellevue Peak (see Chapter 2 for details on locations). Limited additional observations were made in forests bordering two of Dr E. V. J. Tanner's permanent plots (the Mor Ridge forest and Well-developed Mull Ridge forest) so as to obtain a more complete sequence of forest types for certain aspects. A short complementary field phase was carried out in February–March 1997.

1.4 Research objectives and outline of this thesis

The key research objective of the project was to address the question: "What are the causes of forest stunting on wet tropical mountains such as the Blue Mountains?" More specifically:

- What are the contributions of fog and low cloud to forest hydrological and nutrient budgets and how do these affect forest ecological functioning?
- Are the contrasts in forest development related to differences in forest photosynthetic activity?
- Can a model that simulates the effects of rare prolonged dry spells on soil water demonstrate an enhanced sensitivity to drought of low-statured forests and so provide an explanation for the reduction in stature?
- Are the observed contrasts in forest stature caused by differences in nutrient availability between sites? And if so, are these related to differences in (a) decomposition and nitrogen mineralization rates, (b) soil faunal and microbial activity, or (c) other edaphic conditions (intrinsic soil fertility, degree of waterlogging)?
- Are the differences in forest stature reflected by contrasts in nutrient and total polyphenols contents of foliage, litter, and fine roots? And if so, are

phenolic concentrations related to soil acidity, aluminium toxicity, nutrient availability, or soil water levels?

Given the diversity of subjects addressed in this study, a series of papers was adopted as the format to present the respective results. Because this thesis represents a collection of these papers, a certain amount of repetition of the presented material proved unavoidable.

Following the present introduction (Chapter 1), Chapter 2 gives a quantitative characterization of the floristics, biotics and soils of two additional forest sites of contrasting tree stature in comparison to previous work by E. V. J. Tanner [*cf.* *Tanner*, 1977a, b] in the area, along with information on locations, topography and regional climatology. Special attention is paid to the interaction between soil acidity and potentially toxic concentrations of 'free' aluminium in soil water. Chapter 3 discusses contrasts in foliar and fine root chemistry in a series of four forests of gradually increasing stature in relation to tree species, leaf age, humus and soil development and soil water chemistry. Special attention is paid to polyphenol concentrations and possible interactions between aluminium, nitrogen and polyphenol concentrations in leaves and the influence of high soil acidity and aluminium levels on the root system. The climatological conditions in the research area are described in detail in Chapter 4. Both long-term, seasonal patterns and diurnal fluctuations of key climatic parameters are discussed, notably rainfall intensity, deposition of cloud water, and various irradiance-related aspects (PAR, light attenuation in the canopy, albedo). Chapter 5 explores the contrasts in forest water balance components between the two key sites, notably for throughfall, stemflow, and soil water. Long-term changes in soil moisture storage, drainage, and the potential effects of prolonged drought were evaluated using a one-dimensional Soil-Vegetation-Atmosphere-Transfer (SVAT) model. Differences in photosynthetic activity (as indicated by maximum photosynthetic rates), leaf respiration rates, leaf anatomical and stomatal characteristics of various principal tree species in four sites with contrasting forest stature are presented in Chapter 6. Chapter 7 deals with the nutrient fluxes in water at the two key sites. Following a discussion of the changes in chemistry of the water passing through the forest canopy, the litter layer and the soil, the associated nutrient fluxes in rainfall, cloud water, throughfall, stemflow, litter percolate and drainage water and nutrient input–output budgets are presented. In Chapter 8, the nutrient fluxes in litterfall, as well as differences in litter chemistry and standing crop of the two key forests are discussed, whereas detailed information on litter decomposition, nitrogen mineralization, nitrification, soil respiration, and microbial activity is given in Chapter 9. Finally, a synthesis of the results is presented in Chapter 10. The chapter concludes with a selection of recommendations for future research.

2

A QUANTITATIVE CHARACTERIZATION OF THE FLORISTICS, BIOTICS AND SOILS OF TWO MONTANE RAIN FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA*

2.1 INTRODUCTION

With increasing elevation on wet tropical mountains, marked changes in forest structure and physiognomy occur, notably a decrease in stature and average leaf size, whereas the leaves tend to become thicker and harder as well [*Grubb*, 1977]. When characterizing the vegetation on wet tropical mountains, a distinction is often made between relatively tall-statured 'lower montane rain forest' (LMRF) and, generally situated directly above the LMRF belt, smaller-statured 'upper montane rain forest' (UMRF) [*Grubb et al.*, 1963]. This subdivision of montane forest types has been related to the presence of fog and low cloud by *Grubb and Whitmore* [1966] who suggested that LMRF had 'frequent' and UMRF had 'long persistent' cloud cover close to the ground. Later, *Grubb* [1974] stated that tall LMRF could also occur in places that are largely free of fog. Although quantitative criteria of what constitutes 'frequent' or 'long persistent' fog are lacking in the original definitions of *Grubb and Whitmore* [1966], their contention is supported by numerous descriptive studies including bryophyte surveys [*Richards*, 1952; *Van Steenis*, 1961; *Stadtmüller*, 1987; *Proctor et al.*, 1988; *Frahm and Gradstein*, 1991]. Despite the overall importance attached (by most) to the effect of fog on montane forest structure and functioning, there is still no widely accepted explanation of how this is achieved. The multitude of hypotheses that has been advanced to explain the occurrence of stunted montane forest have recently been reviewed by *Bruijnzeel et al.* [1993] in the context of the occurrence of low-statured mossy forest at low elevation on a coastal mountain in Malaysia.

*With L. A. Bruijnzeel, L. Spijkerman, R. Hogervorst, E. V. J. Tanner and H. A. Verhoef. Paper to be submitted in a slightly modified form to the *Journal of Tropical Ecology*.

None of the more common hypotheses examined by *Bruijnzeel et al.* [1993] was capable of explaining the phenomenon. In a more general review of montane forest productivity, *Bruijnzeel and Veneklaas* [1998] drew particular attention to the scarcity of information on the overall carbon economy of tropical montane forests and the influence of climate and soils conditions thereupon.

Comparison of site conditions and ecological processes in stunted and non-stunted montane forests to evaluate the cause(s) of forest stunting is usually hampered by the fact that contrasting climatic conditions between sites at different elevations are not only accompanied by changes in soil type but also in forest species composition [*Proctor et al.*, 1988, 1989; *Veneklaas and Van Ek*, 1990; *Grieve et al.*, 1990; *Bruijnzeel et al.*, 1993; *Pendry and Proctor*, 1996a, b; *Liebermann et al.*, 1996]. Therefore, there is merit in a 'lateral' comparison of forests of contrasting stature having similar species assemblages experiencing similar climatic conditions but contrasting edaphic conditions [*Hetsch and Hoheisel*, 1976; *Tanner*, 1977a]. A striking example of the latter is found in the Blue Mountains of Jamaica at *c.* 1600 *m* a.s.l. along a ridge between John Crow Peak and Sir John Peak, where patches of short-statured (5–7 *m*) forest on deep (0.3–>0.5 *m*) acid Mor-type humus occur side by side with taller (12–17 *m*) forest on less acid Mull-type humus [*Grubb and Tanner*, 1976; *Tanner*, 1977a]. In the early years of the century *Shreve* [1914] ascribed the differences in forest stature between tall ravine forest, intermediate-statured windward slope forest and shorter-statured ridge top forests in the area mainly to differences in atmospheric humidity (notably the occurrence of fog) whereas *Tanner* [1977a, 1985] and *Healey* [1990] rather emphasized contrasts in soil fertility. *Bruijnzeel* [1989b], on the other hand, drew attention to the fact that atmospheric additions of nutrients in the area greatly exceeded amounts actually taken up by the vegetation and incorporated in stemwood [*cf. Tanner*, 1985], suggesting that either the nutrients become immobilized upon entering the soil or that the trees are unable to make optimum use of the nutrients [*cf. Bruijnzeel et al.*, 1993]. To test the alternative hypothesis, a study of the water and nutrient dynamics of two nearly adjacent upper montane forests of contrasting stature at 1809–1824 *m* a.s.l. near Bellevue Peak in the Blue Mountains of Jamaica was initiated in late 1994.

The aim of the present chapter is threefold: (i) to provide additional information on the physical, (hydro)chemical and biotic (micro- and meso-fauna) characteristics of Mor- and Mull-type soils as a supplement to the preliminary characterizations by *Grubb and Tanner* [1976] and the nutrient extraction data of *Tanner* [1977a]; (ii) to provide a basic description of the two study plots, thereby placing them in the context of the ridge-top forest types distinguished earlier by *Tanner* [1977a, 1980b] and serving as a point of reference for the remaining chapters of this thesis; and (iii) to test various hypotheses on the causes of forest stunting against the new evidence presented here.

2.1.1 Study sites

Although developed under comparable geologic and climatic conditions, montane forests above *c.* 1300 *m* a.s.l. elevation in the Blue Mountains may show marked contrasts in stature, soil humus development and ecological functioning [*Tanner*, 1977a, 1980a, b, 1981]. Two forest sites of contrasting stature were selected on a SW-orientated spur (18° 05' 29" N; 76° 38' 57" W) between Sir John Peak (1900 *m* a.s.l.) and Bellevue Peak (1849 *m* a.s.l.), the distance between the latter and the sites being less than 150 *m* (Fig. 2.1).

The two forests are considered to represent intermediate stages in a sequence of upper montane forest types with increasingly acid humus and topsoil (pH 4.4–3.0) and a gradual reduction in forest stature from so-called 'well-developed' Mull forest (WMull, canopy height 12–17 *m*) to stunted Mor forest (5–7 *m*) as identified by *Tanner* [1977a, 1980b]. The shorter-statured forest of the two selected sites is situated at 1824 *m* elevation on a ridge top and can be classified as 'moderately-developed' Mor forest (MMor, main canopy height 5–8 *m*) on the basis of its stature, species composition, epiphytic biomass and humus type. The taller forest of the two (7–12 *m*) is situated on a near-level slope section on the NW-side of the ridge at 1809 *m* elevation and can be classified as 'poorly-developed' Mull forest (PMull), (E. V. J. Tanner, *personal communication*, 1995). Although the lateral distance between the sites is less than 30 *m*, the MMor site is better exposed to the prevailing southeasterly winds (Fig. 2.1, *cf.* Chapter 4) whereas the taller PMull forest remains relatively sheltered throughout the day.

2.1.2 Regional geology and geomorphology

The geology of the western Blue Mountains is complex. Granodiorite as well as andesites and sedimentary rocks (mostly volcanic sandstones, mudstones, shales and conglomerates of the Blue Mountain Volcanics and the Blue Mountain Shale complexes) occur [*Dalling*, 1992]. Many active faults dissect the area, creating a typically block-faulted landscape with distinct 'steps' in the ridges. In this tectonically active setting, the combination of steep slopes, fractured geological strata, tremors and high rainfall (including occasional hurricanes) creates a high landslide potential. Mass wastage, therefore, is the major mechanism of denudation in the area [*Dalling*, 1992], supplemented by surface erosion on the steepest slopes in deforested areas [*McDonald*, 2000].

The soils derived from the respective rock types vary in acidity but their topsoils are generally highly porous. Their overall fertility is low to moderate, depending on the degree of leaching, but N and P are generally low [*Grubb and Tanner*, 1976; *Bellingham*, 1993]. On steep slopes, soils are shallow and stony whereas on more stable sites (including ridge tops) yellowish brown cambisols (FAO soil classification) have developed. Locally, accumulations of acid mor humus are found above shallow mineral soils, notably on isolated knolls [*Grubb and Tanner*, 1976; *Spijkerman*, 1996]. The soils of the two study plots that will be discussed in detail below, and of E. V. J. Tanner's Mor Ridge and Well-

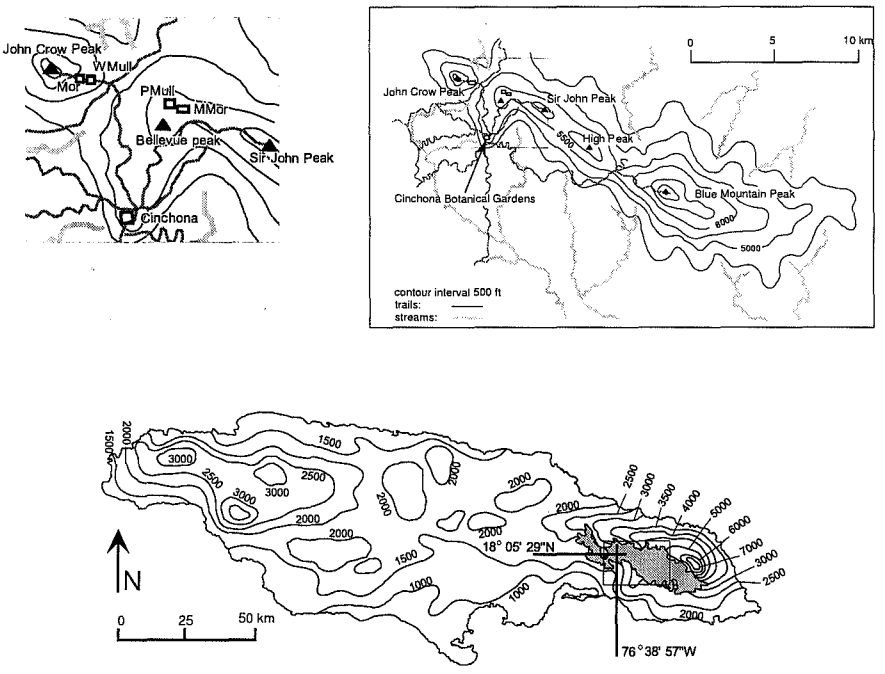

Figure 2.1: Map of Jamaica showing annual isohyetal patterns (*mm*) and the Blue Mountain range (in grey). Insets display the location of the study sites (boxes) and the meteorological station (Bellevue Peak, 1849 *m* a.s.l.). Rainfall figures represent averages over 1951–1980. After *National Meteorological Service of Jamaica* [1986]; inset based on *Shreve* [1914].

developed Mull Ridge forests, are all considered to have derived from andesitic rocks [*Spijkerman*, 1996].

2.1.3 Climate

Regional climate
The climate within the ESE-orientated Blue Mountain range (Fig. 2.1) is strongly influenced by the northeasterly trade winds and the warm waters (25–28 °C) of the surrounding seas. Above 1,000 *m* a.s.l. Jamaica's tropical maritime climate (Köppen type A2m) gives way to a tropical montane climate (type Cfi). Annual rainfall in eastern Jamaica varies from less than 750 *mm* on the south coast to over 7000 *mm* on the northeastern (windward) slopes of the Blue Mountains (Fig. 2.1). Interpolation between the average isohyets suggests an annual

rainfall of *c.* 2850 *mm* for the research area (Fig. 2.1). The nearest rainfall station is at Cinchona Botanical Gardens, which is situated at 1500 *m* a.s.l. at a distance of *c.* 3 *km* towards the SW. It receives, on average, *c.* 2275 $mm\,yr^{-1}$ (1901–1990; range 905–4464 $mm\,yr^{-1}$; J. R. Healey, *personal communication*). Annual variability is large. Rainfall is also unevenly distributed over the year: October and November are normally wet (>350 *mm* each) with a secondary peak in May and June, whereas March and July are relatively dry (<90 *mm* each; Fig. 2.2). Maximum rainfalls are generally associated with cold fronts migrating from North America during the winter months or with tropical storms during the late summer [*National Meteorological Service of Jamaica*, 1986], with mean monthly totals at Cinchona exceeding 175 *mm* for the August–December period (maximum 2416 *mm* in November 1909; *J. R. Healey, personal communication*). Between 1901 and 1990, 15 % of all months at Cinchona had low rainfall (<50 *mm*) and 1.4 % had rainfall totals of less than 10 *mm*. Two long dry periods occurred, viz. 30 days in 1986 and 39 days in 1987 (*J. R. Healey, personal communication*). Showers at Cinchona are usually of short duration (approximately 1 *h*) and tend to fall in the mid-afternoon whereas minimum rainfall occurs at night [*Shreve*, 1914]. Such a pattern suggests a convective mechanism coupled with orographic influences (*cf.* Fig. 2.1 and Chapter 4).

Temperatures in the Blue Mountains are highest in June and August and lowest in December to February, though seasonal fluctuations are suppressed by the moderating influence of the surrounding seas. Temperatures are subject to the local orographic situation and show a regional mean lapse rate of *c.* 0.65 °C per 100 *m* rise in elevation. At Cinchona the average monthly maximum temperatures vary within 2 °C of the annual mean maximum temperature of 22 °C *vs.* 31 °C at the south coast (1951–1980; *National Meteorological Service of Jamaica* [1986]). Corresponding values for average monthly minimum temperatures are 13.5 °C and 24.0 °C. During the year fluctuations of monthly average temperatures are small (<4 °C between the coldest and warmest month) but diurnal ranges can exceed 11 °C in the mountainous interior of the island. Mean monthly relative humidity at noon is close to 85 % (80–90 %) at Cinchona *vs.* 64 % (60–68 %) at the south coast, with relatively little seasonal variation.

Moisture-laden trade wind convection often produces fog and low cloud, particularly on northerly (windward) slopes between 10:00 and 16:00 *h*, but rarely at night [*Shreve*, 1914]. Clouds develop on the ridges and descend towards the leeward areas in the course of the afternoon. Monthly mean sunshine duration at Cinchona is 4.3 $h\,d^{-1}$ (range 3.9–5 $h\,d^{-1}$; 1951–1980; *National Meteorological Service of Jamaica* [1986]) compared to over 8 $h\,d^{-1}$ (7.1–8.8 $h\,d^{-1}$) in the southern coastal zone. On the south side of the Blue Mountains the prevailing trade winds have a persistently easterly to south-easterly direction, but may be altered locally by land-sea wind interactions during the daytime. Although outside the main track of tropical storms, Jamaica was affected by 13 major hurricanes since 1871, on average once every 15 years [*Bellingham*, 1993]. Within the last 20 years, two major hurricanes, viz. Allen in 1980 and Gilbert in 1988, have passed Jamaica.

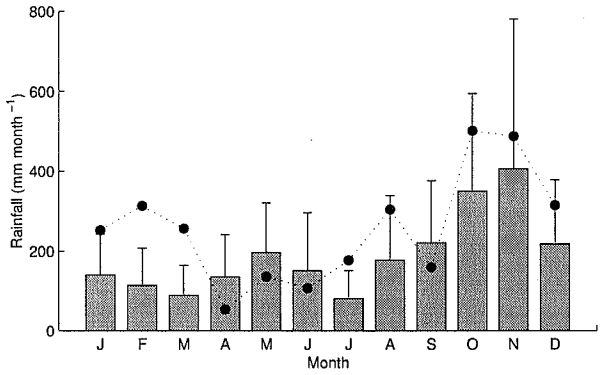

Figure 2.2: Long-term (1901–1990) average monthly rainfall (bars) at Cinchona (1500 m a.s.l.; *J. R. Healey, personal communication*) and monthly totals at Bellevue Peak in 1995 (dots). Vertical lines represent one standard deviation from the mean.

Climatic conditions in the study area

A full description of the climatic conditions in the study area as measured at Bellevue Peak (1849 m a.s.l.; Fig. 2.1) during 1995 is given in Chapter 4. Briefly, gross precipitation in 1995 amounted to 3060 mm, distributed over 205 rain days (14.9 $mm\,d^{-1}$). A total of 71 dry periods of 24 h or longer were recorded (mean: 2.3 days; 160 dry days in total). Of these periods 51 were less than 48 hours; the longest continuously dry period lasted 11 days (27 March to 6 April). Rainfall intensities were low: 47 % of all recorded storms showed intensities $\leq$2 $mm\,h^{-1}$ whereas only 11.3 % of the storms had an intensity >10 $mm\,h^{-1}$. The deposition of cloud water was estimated at 3.4 % of the total rainfall for the relatively exposed MMor forest and at 1.4 % for the taller but less well-exposed PMull forest. The research area received an average daily short-wave radiation load of 13.8 $MJ\,m^{-2}$. Due to the formation of clouds the average amount was 47 % less than the potential maximum. The mean daytime (06:00 – 18:00 h) photosynthetic active radiation (PAR) load was estimated at 650 $\mu mol\,m^{-2}\,s^{-1}$. Average daily (24 h) above-canopy air temperature (T) was 15.9 °C. The corresponding mean value for daytime hours was 17.1 °C. Average relative humidity (RH) was $c.$ 85 %, both for 12- and 24-h periods. Average daily wind speeds, as measured 7 m above the low forest canopy at Bellevue Peak, was 4.1 $m\,s^{-1}$. Values dropped to 3.1 $m\,s^{-1}$ during the day and increased to 5.8 $m\,s^{-1}$ at night. The average open-water evaporation rate (E_0; *Penman* [1956]), a convenient measure to characterize overall climatological conditions at a given location, was calculated at 3.0 $mm\,d^{-1}$ (range: 0.4–8.4 $mm\,d^{-1}$) with 83 % of the days exhibiting rates >2 $mm\,d^{-1}$. Incident rainfall (3060 mm) exceeded E_0 (extrapolated to 1 year: 1104 mm) by a factor of 2.8.

2.2 METHODS

2.2.1 FOREST ENUMERATION AND BASIC FOLIAR CHARACTERISTICS

All trees with stem diameter at breast height (d.b.h.) ≥ 5 *cm* (including tree ferns) in the MMor and PMull plots were tagged, measured for their d.b.h. and identified following the nomenclature of *Adams* [1972] with the assistance of Dr E. V. J. Tanner on the basis of bark characteristics and fresh leaves as sampled with pruning equipment in December 1994. Tree height was measured in March 1995 using an extendable measuring pole. Seedlings and saplings (d.b.h <5 *cm*) were not included but a quantitative inventory of understorey species was conducted in May 1995 by Dr T. Goodland, during which species were assigned to three classes of occurrence: 'present', 'common', and 'frequent'. Minor herbs, non-vascular plants and epiphytes found at heights >1 *m* above ground level were not included. In addition, leaf size, leaf thickness, and specific leaf area (SLA) of live foliage taken from eight principal tree species occurring in both forest plots were determined, viz. Euphorbiaceae: *Alchornea latifolia*, *Chaetocarpus globosus*; Clethraceae: *Clethra occidentalis*; Guttiferae: *Clusia* cf. *havetioides*; Cyrillaceae: *Cyrilla racemiflora*; Podocarpaceae: *Podocarpus urbanii*; Ericaceae: *Lyonia* cf. *octandra* and *Vaccinium meridionale*. Twenty to forty mature leaves without signs of herbivory or discolouring were taken from the upper canopy of 4–6 trees per species per site and bulked per tree. Their surface areas were determined by weighing pieces of paper of the same size as the leaves to the nearest 0.001 *g* and converting these to surface areas via a predetermined conversion factor. Values of SLA were obtained by dividing surface area by the corresponding dry weight (measured to the nearest 0.001 *g* after drying to constant weight at 50 ^{o}C). Approximate weighted averages at the plot scale were obtained by weighting the average results for each species on the basis of their relative contribution to total plot basal area. The leaf area index (LAI) of a plot was then estimated by multiplying weighted average SLA times the annual leaf fall over 1995 (see Chapter 8), making adjustments for differences in leaf life span for the respective species as given by *Tanner* [1980a]. Leaf thickness was measured on at least 40–100 healthy mature sun leaves collected in a random manner from 4–6 trees of the following five principal species: *C. racemiflora*, *L. octandra*, *C. globosus*, *A. latifolia*, and *P. urbanii* and bulked per site. Measurements were made using a Mitutoyo dial pipe gauge with a resolution of 0.01 *mm* in the centre of the leaf, next to the main vein.

2.2.2 SOIL BIOTICS

Bacterial and fungal densities were determined on leaves of *L. octandra*, *C. racemiflora*, and *C. occidentalis* contained in 3–4 litterbags per species per plot placed on the forest floor for 136 days (from 21 December 1994 to 6 May 1995), as well as for 7 homogenized single soil samples taken at 5 *cm* intervals down to a depth of 30 *cm* in May 1995. Bacteria were counted in a litter/soil suspension (0.5–2.0 *g*, fresh weight) after staining with 4.0 *mg* DTAF (Fluka Chemie AG CH-9470 Buchs) in 20 *ml* $Na_2HPO_4.2H_2O$—NaCl buffer at pH = 9 of bacterial

cell wall tissue on microscopic slides [*Hogervorst et al.*, 1997]. The actual counting was performed under fluorescent light at 1000× magnification in twenty reticule fields per sample. Fungal hyphae lengths were measured by staining with 20 μl FITC/acetone/H_2O solution (5.0 mg:1 ml:199 ml) of a blended suspension of litter (0.5–2.0 g, fresh weight) in 60 ml McIlvaine-buffer kept at field pH. After filtration (45 μm), twenty random reticule fields were counted for fungal hyphae length under fluorescent light at 250× magnification [*Faber et al.*, 1992].

Soil mesofauna was extracted from 72 litterbags (6 replicates×3 species×2 sites×2 periods) containing the same leaf species as used for the bacterial and fungal counts after 200 and 250 days of exposure on the forest floor using open 'Tullgen-type' funnels [*Van Straalen and Rijninks*, 1982] and forced drying under electric light bulbs. Collections were stored in a 70/5 mixture of alcohol and formaldehyde prior to identification to group level in Amsterdam.

2.2.3 Soil physical and chemical characteristics

Description and sampling procedures

After reconnaissance surveys by auger, soil pits were dug down to (weathered) bedrock directly adjacent to the PMull and MMor forest plots. Two additional pits were dug next to the Mor Ridge and well-developed Mull (WMull) forest plots described by *Tanner* [1977a, 1980b]. Soil monoliths were taken from all four pits for future display at the International Soil Reference and Information Centre (ISRIC), Wageningen, The Netherlands. Soil profile descriptions were made by L. Spijkerman according to the guidelines of *FAO-UNESCO* [1990]. Four to eleven undisturbed soil cores (100 cm^3 each) were collected per horizon for subsequent determination of bulk density, saturated hydraulic conductivity, and soil water retention curves. Single bulk samples were collected in the 4th week of January and the 1th week of February 1996. Samples were taken every 5–10 cm from both the ectorganic and mineral soil horizons for grain size and chemical analyses. The field-moist samples were stored at 4 $^{\circ}C$ in closed plastic bags until transportation by air to Amsterdam. Forest floor litter ($n = 5$) and topsoil material (H/Ah transition layer) were sampled in more replicates (11–13) to assess the variability in pH within and between the four sites.

Additional information on the fertility status of both ectorganic and mineral soil horizons was obtained by sampling the litter percolate and soil moisture in the chief horizons at each of the four forest plots. Water percolating through the litter layer (L-horizon) was collected using 40 cm × 40 cm plates of chemically inert plastic covered with a 1 mm nylon wire mesh connected to dug-in containers via plastic tubing [*Bruijnzeel et al.*, 1993]. Plates were carefully inserted underneath the litter at randomly selected locations ($n = 6$ in both the MMor and PMull plots; $n = 1$ close to each of Tanner's Mor and WMull forests). Litter percolate was taken from the collectors every 6–8 days and bulked to monthly totals from which a sample was taken for chemical analysis. Soil water was extracted using three sets of four vacuum-tube lysimeters [*Hansen and Harris*, 1975] at an initial suction of −50 kPa in the PMull and

MMor forest plots; additional sets (one per plot) were installed in the vicinity of the Mor and WMull forest plots. All tube lysimeters had been thoroughly rinsed with dilute nitric acid and distilled water before installation. The first two extractions were discarded before sampling started. To allow equilibration of the new ceramic cups of the samplers in the Mor and WMull soils (and so improve the representativity of the samples), the first five extractions were discarded [*Hansen and Harris*, 1975; *Rauland-Rasmussen*, 1989]. Samples were taken at 3–4 week intervals between 26 February 1995 and 12 April 1996 and bulked per soil horizon in each plot. Both litter percolate and soil water samples were stored in two clean polyethylene bottles (100 cm^3): one for the determination of pH, electric conductivity and major anions, the other for the analysis of cations, silicon, and phosphate after filtration through a 0.45 μm Millipore filter and acidification with 0.7 ml HNO_3 (65% Suprapure) to a final pH $\leq$2 [*Appelo and Postma*, 1993]. All water samples were stored in the dark at 4 ^oC until transportation by air to Amsterdam (once every 3 months).

Analytical procedures

Grain size distributions were determined on four soil samples per horizon for the fraction $\leq$2 mm with a Fritsch Analysette 22 laser particle sizer following the specifications of *Konert and Vandenberghe* [1997]. Saturated hydraulic conductivity (K_{sat}) was determined using an ICW permeameter in falling- or constant-head mode, depending on the sample's permeability [*Kessler and Oosterbaan*, 1973]. Porosity was measured on the same core samples as used for the determination of K_{sat} by gravimetrically determining the moisture content after 3–7 days of saturation (depending on texture). Soil-water retention curves were determined using the porous-medium and pressure-membrane techniques on undisturbed cores and aggregates, respectively [*Black et al.*, 1965; *Stakman*, 1973]. The water-holding capacity of each horizon was calculated as the difference in volumetric moisture content at field capacity (defined as the soil water suction ψ_m at -10 kPa or $pF = 2$) and the permanent wilting point ($\psi_m = -1.58$ MPa or $pF = 4.2$) [*Stakman*, 1973]. Bulk density was measured by weighing the core samples after 24 h of drying at 105 ^oC.

Soil pH was measured potentiometrically within 4 h after sampling using a Sentron 1002 (ISFET probe) pH meter in 1:5 (ectorganic layers) and 2:5 (mineral horizons) extracts of distilled water (pH_{H_2O}) and 0.01 M $CaCl_2$ (pH_{CaCl_2}) after 1 h of shaking.

Total nitrogen and carbon were determined with a Carlo Erba elemental analyser (NA-1600). Loss on ignition (LOI) was determined by ventilated micro-wave destruction (15 min at 550 ^oC). Water-soluble NH_4 and NO_3 and KCl-extractable NH_4 and NO_3 were determined by colorimetry in 1:1 aqueous extracts and 1 M KCl extracts, respectively, that were shaken overnight, centrifuged and filtered through a 0.2 μm filter [*Keeney*, 1982].

Concentrations of exchangeable cations were determined by spectrophotometry (Perkin-Elmer 5000 AAS); NH_4 by colorimetry (Skalar SFA, modified Berthelot reaction) in non-buffered $BaCl_2$ (0.125 M) extractions (1:25 by weight, shaken for 2 h) after centrifugation and filtration (0.2 μm). Effective cation ex-

change capacity (ECEC) [*Hendershot and Duquette*, 1986; *Amacher et al.*, 1990] was calculated as the sum of $BaCl_2$ extractable bases (including NH_4^+) and exchangeable acidity (determined by titration with 0.02 M NaOH to pH 8.3 in a N_2 atmosphere; *Thomas* [1982]). The carboxyl content of the soil organic material was not included in the sum of ECEC. Base saturation percentage (BSP) was expressed as the sum of extractable bases (Na^++K^++Ca^{2+}+Mg^{2+}) divided by ECEC × 100 % [*Landon*, 1991]. Total elemental concentrations were determined by X-ray diffraction mass spectrometer analysis (Philips PW 1404).

Soil water and litter percolate were analyzed for cations by ICP emission (Perkin-Elmer 6500), except for Na and K (Eppendorf flame photometer). Concentrations of NH_4, SO_4, NO_3, and PO_4 in water samples, aqueous- and KCl-extracts were measured by colorimetry on continuous-flow Technicon/Skalar auto-analyzers, using the modified Berthelot reaction, the methyl-thymol blue, cadmium reduction and absorbic acid reduction methods, respectively. Total N and total P were determined after K_2SO_4/H_2SO_4 digestion; dissolved organic carbon (DOC) was determined with a Skalar SFA auto-analyzer using continuous-flow UV destruction and sulfanylamide coloration reagents. Concentrations of phenolic compounds were measured photometrically using Folin-Ciocalteau reagents [*Box*, 1983]. Absorbance was measured at 760 *nm* relative to a solution series of pure tannic acid powder (Merck, art. nr. 1.00773.0250). Concentrations of phenolic compounds were expressed as tannic acid equivalents ($mg\,\mathrm{TAE}\,l^{-1}$).

Speciation of aluminium species in selected water samples was investigated by thermodynamic computation using the PHREEQC model [*Parkhurst*, 1995] adapted for Al-complexation with aqueous organic material [*Driscoll and Schecher*, 1988]. Samples were selected on the basis of charge balance calculations: elemental analyses were corrected for the presence of organic carboxylate anions (A^-) following *Oliver et al.* [1983] according to:

$$[A^-] = \frac{\overline{K}[C_T]}{\overline{K} + [H^+]} \tag{2.1}$$

where $\overline{K}$ is the pH-dependent dissociation constant and C_T the total organic acid concentration or carboxyl content of the aquatic humic substances, *i.e.* the potentially complexing part of total DOC. Initially set at 10 $\mu mol_c\,mg^{-1}$ DOC [*Oliver et al.*, 1983], C_T was allowed to vary between 8–12 $\mu mol_c\,mg^{-1}$ DOC if charge balance differences prior to the speciation calculations exceeded ± 10 % of the summed cations. Samples that could not be corrected within these ranges were rejected; those remaining were averaged per chief horizon. Colloidal aluminium and very strong aluminium-organic complexes had to be neglected; all Al determined by ICP emission was assumed to be monomeric.

2.3 RESULTS

2.3.1 FOREST STRUCTURE, FLORISTICS AND FOLIAR CHARACTERISTICS

A tabular overview of several basic forest structural characteristics of the MMor and PMull sites is given in Table 2.1, together with the corresponding data for the Mor, Mull, and Well-developed Mull (WMull) forests of *Tanner* [1977a, 1980b] located about 2 *km* towards the West at *c.* 1600 *m* a.s.l. (*cf.* Fig. 2.1). The gradual reduction in maximum canopy height in the sequence WMull>Mull>PMull>MMor>Mor forest sequence is evident. Average tree heights in the present two sites were intermediate at 7.4 $\pm$ 1.8 *m* (PMull) and 5.7 $\pm$ 1.3 *m* (MMor), (*cf.* Fig. 2.3 and Fig. 2.4). Species richness shows a similarly negative trend for the same sequence (roughly halved) from WMull to Mor forest, although the number of species and the basal areas found in the present two plots were underestimated somewhat because of their smaller plot size (0.024 *ha* for the MMor; 0.03 *ha* for the PMull *vs.* 0.08–0.10 *ha* for the Mor and (W)Mull) and because of the use of a slightly larger enumeration limit (d.b.h. $\geq$5 *cm* at PMull and MMor *vs.* g.b.h. $\geq$10 *cm* (d.b.h. $\geq$3.2 *cm*) for the Mor, Mull and WMull plots; *Tanner* [1977a, 1980b]). The effect will be small in the PMull because few trees had a d.b.h. of $3.2<x<5$ *cm* but may be more marked in the case of the MMor plot which had an average d.b.h. of 8.5 *cm*. The intermediate character of the PMull and the MMor plots is highlighted further by the number of trees with multiple stems and the tree/trunk ratio, both of which increase markedly from WMull to Mor forest (Table 2.1).

A first estimate of the leaf area index (LAI, m^2m^{-2}) of the PMull and MMor forest plots was obtained by multiplying weighted average specific leaf area (SLA; Table 2.1) times annual leaf fall (see Table 8.1 in Chapter 8) and correcting for the deviation in leaf life span from a 12-month period [*cf. Roberts et al.*, 1999]. Values for the latter were taken from *Tanner* [1980b] and assumed to be identical for the Mull and PMull sites (13.2 *months*) and the Mor and MMor sites (17.6 *months*). The exercise was repeated for the Mor and WMull sites using SLA and leaf fall data given by *Tanner* [1980b, a] (leaf fall for 1974/75; 491 and 532 $g\,m^{-2}yr^{-1}$ in the Mor and Mull). The average SLA of the PMull was almost the same as for the more stunted MMor and Mor forests but much smaller than the value found for the tall WMull forest (Table 2.1).

Despite the rather crude manner in which it was obtained, the LAI of the MMor forest resembles that derived for the Mor forest (4.0 m^2m^{-2}). It is also very similar to the 4.1 m^2m^{-2} for tree leaves obtained by destructive sampling in the Mor forest by *Tanner* [1980b] (the canopy LAI was estimated at 4.4 m^2m^{-2}). Repeating the exercise for the WMull forest using the 1977/1978 leaf-fall for the Mull forest (563 $g\,m^{-2}yr^{-1}$) in combination with the mean SLA given by *Tanner* [1980b] (92 $cm^2\,g^{-1}$) gave an LAI of 5.7 m^2m^{-2}. This is somewhat higher than the 5.1 m^2m^{-2} reported for tree leaves by *Tanner* [1980b] based on destructive sampling (canopy LAI: 5.3 m^2m^{-2}). However, rates of leaf-fall obtained by *Tanner* [1980a] did include reproductive parts (which may be estimated at *c.* 10 % of total leaf litter, *cf.* Chapter 8). Correcting for this

Table 2.1: Species richness, main canopy height, basal area (BA), number of trees per hectare, number of trees with multiple trunks (TWMT) and trunk/tree ratios for trunks with diameter at breast height ≥ 5 *cm*; specific leaf area (SLA), and leaf area index (LAI) for the WMull (0.10 *ha*), Mull (0.10 *ha*), PMull (0.03 *ha*), MMor (0.024 *ha*) and Mor (0.08 *ha*) sites. Data for the WMull, Mull, and Mor forest are from *Tanner* [1977a, 1980b]; tree density data for the WMull are based on *E. V. J. Tanner, personal communication* 1996.

Forest	Species per site	Height m	BA $m^2 ha^{-1}$	Trees ha^{-1}	TWMT	Trunk/tree ratio	SLA $cm^2\,g^{-1}$	LAI -
WMull	34	13–17	77.9	6200	175	1.03	92[1]/78[2]	5.1[3]
Mull	34	8–13	65.4	5200	500	1.13	-	-
PMull	23	7–12	53.1	4400	567	1.19	60	3.4[4]
MMor	10	5–8	44.4	6043	1043	1.29	61	4.1[4]
Mor	16	5–7	64.7	4900	1500	1.49	58[1]/60[2]	4.1[3]

[1] *Tanner* [1980b]; [2]this study; [3]trees only, based on destructive sampling [*Tanner*, 1980b]; [4]this study, SLA times leaf litterfall.

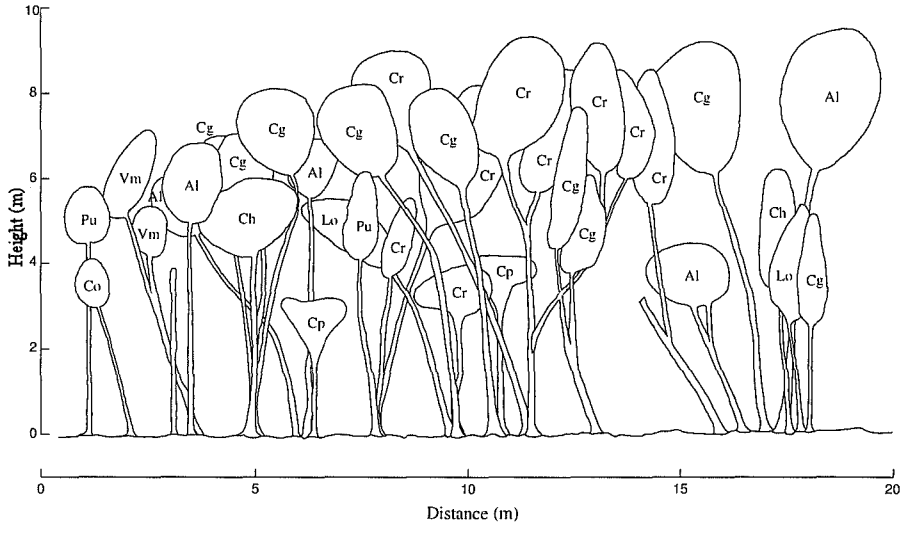

Figure 2.3: Profile diagram of 20×4 m of medium-statured PMull forest at 1809 m in the Blue Mountains, Jamaica. Symbols for trees over 5 *cm* d.b.h.: Al, *Alchornea latifolia*; Ch, *Clusia* cf. *havetioides*; Cr, *Cyrilla racemiflora*; Cg, *Chaetocarpus globosus*; Co, *Clethra occidentalis*; Lo, *Lyonia* cf. *octandra*; Cp, *Cyathea pubescens*; Po, *Podocarpus urbanii*; Vm, *Vaccinium meridionale*. After *Bronckers and van Hesteren* [1995].

overestimation results in an LAI identical to the one obtained using destructive sampling (5.1 $m^2 m^{-2}$). In view of the plausible LAI values obtained for the Mor, MMor and Mull forests, the low 3.4 $m^2 m^{-2}$ calculated for the PMull forest is surprising and must be considered an anomaly. We will come back to this point in Section 2.4.1.

Table 2.2 lists the relative contributions of the principal tree species to total plot basal area in the respective forest types (excluding the WMull whose composition is nearly identical to that of the Mull forest [*Tanner*, 1980b]). A species was considered 'principal' if it represents $\geq$1 % of the total basal area in each of the four forests or $\geq$10 % in at least one of the forests.

As noted earlier for species richness and plot basal area (Table 2.1), the figures in Table 2.2 are influenced to some extent by the relatively small size of the PMull and MMor plots compared to E. V. J. Tanner's Mor and Mull plots and by the slightly different enumeration limit used in the present study. As such, the rather low values obtained for *Clethra occidentalis* in the PMull and for *Alchornea latifolia* and *Chaetocarpus globosus* in the MMor may be partly artificial. Despite such limitations various overall differences in the species compositions of the Mor and Mull forests are demonstrated by Table 2.2, including a gradual increase in the occurrence of *Clusia* cf. *havetioides* in the Mull to Mor sequence; the dominance of *Lyonia* cf. *octandra* in the more stunted forest types *vs.* that of *Clethra occidentalis* and *Podocarpus urbanii* in the (W)Mull forests. The presence of the introduced species *Cinchona pubescens* in the MMor forest (5.3 %, Table 2.2) suggests a certain degree of disturbance. A comparison of the average heights and diameters at breast height (d.b.h.) of the 7–8 principal tree species in the PMull and MMor forests reveals that five out of seven species were taller in the PMull forest. However, this was not paralleled by larger d.b.h. values, except for *Chaetocarpus globosus* (12.6 *vs.* 8.4 *cm*; Table 2.3).

No significant differences were found between the two forest types for average leaf size, weight, and SLA of seven principal tree species, although significantly increased leaf thickness was observed for three out of four species in the MMor forest (one-tailed *t-test*, P< 0.01). Conversely, leaves of *Lyonia* cf. *octandra* were found to be thicker in the PMull forest (P< 0.01; Table 2.4). The leaves of the majority of the principal species in both forests were microphylls (<2000

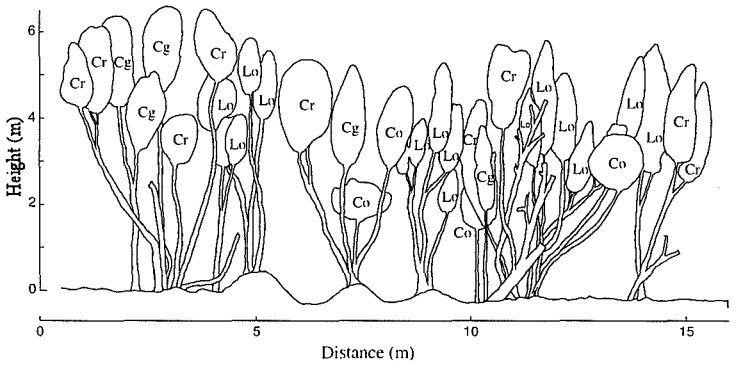

Figure 2.4: Profile diagram of 16×4 *m* of low-statured MMor forest at 1824 *m* in the Blue Mountains, Jamaica. Symbols for trees over 5 *cm* d.b.h.: Cr, *Cyrilla racemiflora*; Cg, *Chactocarpus globosus*; Co, *Clethra occidentalis*; Lo, *Lyonia* cf. *octandra*. After *Bronckers and van Hesteren* [1995].

Table 2.2: The percentage contribution of principal tree species to the total basal areas (BA) of trees with d.b.h. ≥ 5 *cm* (MMor and PMull plots) or d.b.h. ≥ 3.2 *cm* (Mor and Mull plots; *Tanner* [1977a]).

Species	Mull	PMull	MMor	Mor
	Contribution to plot basal area (%)			
Principal species				
Alchornea latifolia	5.5	15.1	0.7	9.9
Chaetocarpus globosus	4.8	16.0	8.9	17.0
Clethra occidentalis	21.7	6.3	5.7	3.8
Clusia cf. *havetioides*	0.1	1.6	3.3	9.3
Cyrilla racemiflora	21.9	20.0	23.4	13.7
Ilex macfadyenii	0.4	3.2	0.4	2.4
Lyonia cf. *octandra*	4.9	12.7	45.5	36.8
Podocarpus urbanii	14.8	8.0	-	0.8
Vaccinium meridionale	2.3	1.8	6.6	2.8
Hedyosmum arborenscens	10.1	0.4	-	-
Additional species				
Cinchona pubescens	-	-	5.3	-
Schefflera sciadophyllum	0.2	0.3	0.2	0.5
Ilex obcordata	-	1.3	-	2.7
Mull species				
Cyathea furfuracea	0.7	1.8	-	-
Cyathea pubescens	1.3	1.6	-	-
Eugenia virgultosa	0.7	1.1	-	-
Myrsine coriacea	-	2.1	-	-
Bumelia montana	2.1	-	-	-
Dendropanax arboreus	-	2.8	-	-
Dendropanax pendulus	1.2	-	-	-
Haenianthus incrassatus	1.0	-	-	-
Turpinia occidentalis	1.1	-	-	-
Solanum punctulatum	1.4	-	-	-
other species	3.8	3.9	0.0	0.9

Table 2.3: Average values (and their standard deviations in parentheses) of height (cm) and diameter at breast height (cm) of seven principal tree species in the PMull and MMor forests.

Species	Height (cm)						Diameter at breast height (cm)					
	PMull			MMor			PMull			MMor		
	range	avg.	(s.d.)	range	avg.	(s.d.)	avg.	(s.d.)	max.	avg.	(s.d.)	max.
Alchornea latifolia	520–1115	796	(145)	570–670	620	(50)	10.2	(5.4)	29.1	6.8	(0.8)	7.5
Chaetocarpus globosus	485–960	768*	(137)	440–810	572	(85)	12.6*	(4.7)	23.0	8.4	(2.6)	16.1
Clethra occidentalis	415–880	719*	(127)	470–750	612	(80)	8.4	(2.1)	11.9	7.1	(1.9)	11.2
Clusia cf. *havetioides*	440–780	610*	(114)	310–465	386	(63)	7.2	(1.7)	10.1	7.4	(2.6)	13.7
Cyrilla racemiflora	525–1150	801	(210)	310–820	576	(156)	13.6	(7.3)	29.1	9.2	(2.2)	13.2
Lyonia cf. *octandra*	460–1075	818*	(179)	245–850	584	(126)	11.1	(4.5)	20.7	8.6	(2.4)	14.7
Vaccinium meridionale	590–775	668*	(61)	380–745	530	(99)	8.8	(1.9)	10.6	7.1	(1.6)	11.0

* significantly larger mean value ($\alpha = 5\%$, $P < 0.01$; *t-test*, unpaired, one-tail) for a species in the PMull forest compared to the same species in the MMor forest.

Table 2.4: Basic leaf characteristics of seven principal tree species in the PMull and MMor forests. Average values (and their standard deviations in parentheses) for area, weight, and specific leaf area (SLA, $cm^2\,g^{-1}$) of $40 \leq n \leq 100$ mature, sunlit leaves per species per site. Leaf thickness at canopy height is based on *Chardonnens* [1996] using $30 \leq n \leq 270$ leaves per tree species per site.

Species	Area (cm^2)				Weight (g)				SLA ($cm^2\,g^{-1}$)				Thickness (μm)			
	PMull		MMor		PMull		MMor		PMull		MMor		PMull		MMor	
Alchornea latifolia	36.1	(9.6)	37.7	(10.7)	0.62	(0.20)	0.63	(0.20)	57.8	(25.6)	59.7	(4.8)	-	-	-	-
Chaetocarpus globosus	6.2	(1.5)	6.8	(1.6)	0.14	(0.04)	0.11	(0.03)	56.1	(7.2)	50.4	(3.2)	240	(31)	387*	(49)
Clethra occidentalis	35.1	(10.2)	26.9	(7.7)	0.51	(0.18)	0.36	(0.07)	69.0	(12.7)	74.0	(18.6)	216	(31)	233*	(24)
Clusia cf. *havetioides*	53.0	(4.9)	62.8	(7.8)	1.57	(0.19)	1.91	(0.35)	33.7	(3.5)	33.0	(3.1)	-	-	-	-
Cyrilla racemiflora	11.73	(1.9)	9.0	(1.3)	0.20	(0.05)	0.15	(0.02)	57.7	(8.5)	61.8	(10.8)	282	(68)	322*	(61)
Lyonia cf. *octandra*	7.8	(2.0)	9.5	(2.7)	0.14	(0.03)	0.16	(0.05)	57.7	(4.9)	60.3	(7.5)	316*	(47)	278	(38)
Vaccinium meridionale	3.4	(0.1)	2.9	(0.4)	0.05	(0.00)	0.05	(0.01)	65.1	(1.9)	63.9	(3.6)	-	-	-	-

* significantly larger mean value ($\alpha = 5\%$, $P < 0.01$; *t-test*, unpaired, one-tail) for a species in the PMull forest compared to the same species in the MMor forest.

mm^2), with those of *Clethra* and *Alchornea* belonging to the notophyll size class (2000–4500 mm^2) and only those of *Clusia* cf. *havetioides* attaining mesophyll size (>4500 mm^2) (Table 2.4).

For both forests, all species with individuals of d.b.h. $\geq$5 *cm* were also present in the <5 *cm* d.b.h. class. In contrast to the understorey in the Mor site [*Tanner*, 1977a], *Clusia* cf. *havetioides* and *Lyonia* cf. *octandra* seedlings were present in the MMor but not in large numbers (Table 2.5). The presence of *Pittosporum undulatum* Vent. (Pittosporaceae) saplings in the understorey of the PMull and MMor forest is disturbing. This aggressive invasive species, native to south-eastern Australia and introduced to the Cinchona Botanical Gardens, germinates under conditions of restricted light, forms very dense canopies and is assumed allelopathic [*Dalling*, 1992]. As a result, *P. undulatum* is taking over native forest in the study area at an alarming rate. Large individuals (d.b.h. >10 *cm*) are already found in close proximity to the research area. In time, *Pittosporum undulatum* may become a dominant species in both study sites.

2.3.2 Soil biotics

Table 2.6 summarizes the observations on bacterial densities and fungal lengths in natural litter and litterbags containing *Cyrilla racemiflora*, *Lyonia* cf. *octandra* or *Clethra occidentalis* leaves after exposure in the field for 136 days in the PMull and MMor forest plots. Bacterial densities in the PMull litter were 2 to 8 times higher than in the MMor, although counts in the natural litter from the two plots were virtually equal. Fungal lengths in *Cyrilla racemiflora* and *Lyonia* cf. *octandra* litterbags were not different between the two sites but those in *Clethra occidentalis* litter in the Mull were more than twice the value observed in the MMor, although standard errors were large (> 50 %; Table 2.6). Bacterial densities in the actual litter layer were of the same order of magnitude as found for the litter bags but counts of fungal lengths were very much smaller, mainly because fungi were masked by soil particles during determination (but possibly also because of sample heterogeneity in terms of species composition and litter age).

As shown in Fig. 2.5A, bacterial densities in the top 30 *cm* of the PMull litter and soil profile (comprising the LFH–Ah–Bh horizons of Appendix A) were highest in the top 2 *cm* and below 20 *cm*, with intermediate densities in between. Bacterial densities in MMor material (LFH-horizons; Appendix A) decreased more or less steadily with depth. The corresponding patterns for fungal length contrasted between sites, with a more or less linear (through irregular) decrease with depth in the PMull and an exponential decrease in the MMor (Fig. 2.5B). Details on litter decomposition rates and mechanisms in the two forest plots are given in Chapter 9.

Table 2.7 gives an overview of the species richness and mean density values for 30 principal soil fauna groups as observed in the litterbags. The contrast in fungal biomass between the two sites (highest biomass in the PMull) is paralleled by the distribution of fungivores such as mites and springtails (*Cryptostigmata* and Collembola). In turn, the latter are tentatively related to the number of

Table 2.5: Understorey species present within the PMull and MMor plots and in an area extending 5 *m* beyond the plot boundaries. Relative distribution is indicated as: present (p), common (c), or frequent (f). All trees and woody plants with d.b.h. <5 *cm* are included; non-vascular plants, epiphytes found at heights above 1 *m* from the forest floor, and minor herbs were excluded. Inventory by Dr T. Goodland, May 1995.

Trees and woody plants	PMull	MMor	Herbs and climbers	PMull	MMor
Alchornea latifolia	p	p	*Blechnum lineatum*	c	c
Cassia viminea	p	-	*Chusquea abietifolia*	f	-
Chaetocarpus globosus	p	-	*Columnea hirsuta*	-	p
Cinchona pubescens	p	c	*Glychenia spp.*	-	p
Cinnamomum montanum	p	-	*Hedychium gardnerianum*	p	p
Citharexylum caudatum	p	-	*Hymenophyllum spp.*	f	-
Clethra occidentalis	c	c	*Lepanthes spp.*	p	-
Clusia cf. *havetioides*	p	p	*Maratate* (fern)	p	-
Cyathea furfuracea	p	-	*Odontosoria spp.*	p	p
Cyathea pubescens	p	-	*Ophioglossum spp.*	f	f
Cyrilla racemiflora	p	p	*Orchid spp.*	-	p
Dendropanax arboreus	p	-	*Peperomia crassicaulis*	p	p
Dendropanax nutans	p	-	*Rhynchospora eggersiana*	p	-
Dendropanax pendulus	p	-	*Rhynchospora jamaicensis*	p	-
Euginia alpina	p	p	*Smilax balbisiana*	-	p
Euginia virgultosa	f	p	*Tilliandsia complanata*	-	p
Guarea glabra	f	-	*Trichomanes spp.*	p	-
Hedyosmum arborenscens	c	-	*Vriesea incurva*	p	p
Ilex macfadyenii	p	c			
Ilex nitida	-	c			
Ilex obcordata	p	p			
Lyonia cf. *octandra*	p	p			
Mannetia lygistum	p	-			
Mecranium purpurascens	c	p			
Meriania purpurea	p	-			
Miconia quadrangularis	-	p			
Miconia rigida	p	p			
Myrsine coriacea	c	p			
Palicourea alpina	c	-			
Pittosporum undulatum	f	c			
Podocarpus urbanii	c	p			
Psychotria corymbosa	c	p			
Rhamnus sphaerospermus	c	-			
Schefflera sciadophyllum	p	p			
Turpinia occidentalis	p	-			
Vaccinium meridionale	p	p			
Vernonia pluvialis	p	-			
Viburnum spp.	-	p			
Wallenia crassifolia	p	-			

Table 2.6: Average bacterial density and fungal hyphae length (and their standard deviations) in litterbags containing leaves of *Lyonia* cf. *octandra*, *Cyrilla racemiflora* or *Clethra occidentalis* after 136 days of field exposure and in natural mixed litter in the PMull and MMor forest plots. Density values are expressed as number- (bacteria) or metres (fungi) per gram dry weight substrate.

Forest	Bacterial density [no.$\times 10^9 g^{-1}$]			
	Natural litter	*Lyonia*	*Cyrilla*	*Clethra*
PMull	0.90	0.68±0.14	0.98±0.42	5.30±2.33
MMor	0.92	0.35±0.33	0.33±0.20	0.67±0.32

Forest	Fungal hyphae length, [$m\, g^{-1}$]			
	Natural litter	*Lyonia*	*Cyrilla*	*Clethra*
PMull	0.52	5.25±1.56	11.89±6.41	7.07±4.84
MMor	2.26	4.24±1.33	10.87±3.61	3.24±1.73

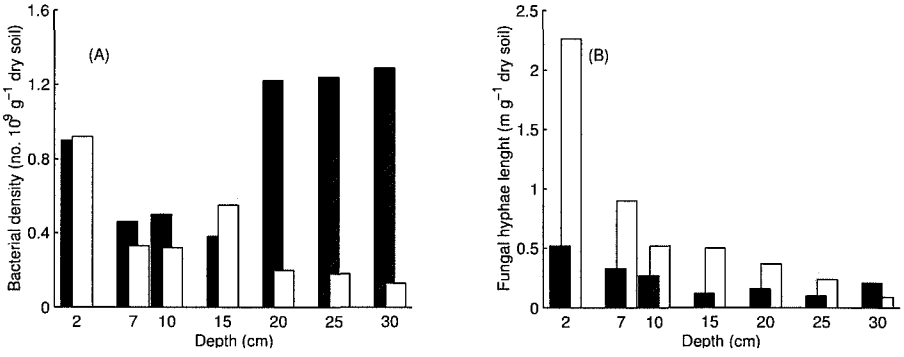

Figure 2.5: (A) Distribution of bacterial density (no.$\times 10^9 g^{-1}$ dry soil) and (B) fungal hyphae length ($m\, g^{-1}$) with depth (as measured from the forest floor) in PMull (solid bars) and MMor (white bars) soil profiles. After *Elbers* [1996].

predators (mainly *Staphylinidae*) among the Coleoptera (beetles), as *Staphylinidae* made up to 33 % of the total number of Coleoptera in the MMor but 80 % in the PMull. The contrasts in densities of Isopoda (woodlice), Diplopoda (millipedes), and Diptera larvae (all higher in the PMull) probably explain the higher litter decomposition activity observed in the PMull (Chapter 9). Both Hymenoptera (ants and wasps) and adult Diptera (flies and midges) were present in considerable numbers in both forests (Table 2.7), despite ample possibilities for their escape from the litterbags. Formicidae (ants) were found only in very small numbers, Isoptera (termites) were distinctly absent from the litterbags.

2.3.3 Soil physical and chemical characteristics

Detailed descriptions of the soil profiles underlying the PMull and MMor forest plots, as well as those for the WMull and Mor sites of *Tanner* [1977a, 1980b], are given in Appendix A. A schematic representation of their horizonation is given in Fig. 2.6. The loamy soils of the PMull and WMull sites are classified as Dystric cambisols and the siltier soils of the MMor and Mor sites as Folic histosols [*FAO-UNESCO*, 1990]. The two Mull profiles are characterized by relatively thin L, F and H horizons (typically *c.* 2 *cm* of fresh litter and *c.* 4 *cm* of fermented and fragmented litter and humus) whereas the two Mor profiles have a 30–50 *cm* thick ectorganic layer (Fig. 2.6) which shows great spatial variability in thickness [*Spijkerman*, 1996].

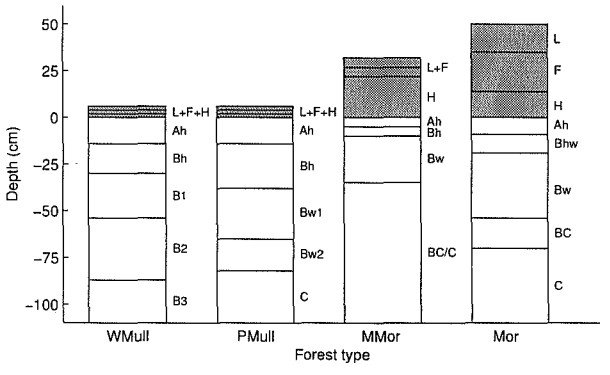

Figure 2.6: Schematic representation of WMull, PMull, MMor, and Mor soil profiles. Ectorganic layers (grey sections) are indicated above the zero reference depth and mineral soil horizons (white sections) below it.

Soil physical characteristics

A tabular overview of some basic physical characteristics of the soils of the four forest plots is given in Table 2.8. The Mor profiles show an increase in sand content with depth and a strong decrease in clay content below the Ah-horizon. By contrast, the WMull profile shows the reverse pattern, *i.e.* decreasing sand content and increasing clay content with depth. The gravel/stone contents in

Table 2.7: Species richness and population density for 30 principal soil fauna groups in litterbags containing foliar material of *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, or *Clethra occidentalis*. Litterbags (6 per species) were removed after 200 and 250 days of field exposure. Density values (number of individuals) represent (36 (6 replicates×3 species×2 periods) bag averages, standardized to no. per m^2 per 100 g residual substrate. The numbers of observed species represent totals over 36 bags. Nematoda (roundworms) and Enchytraeidea (potworms) were not included in the identifications.

Class and Order	Sub-order	PMull		MMor	
		Species	Density	Species	Density
		no.		*no.*	
Annelida (segmented worms)					
Oligochaeta (earthworms only)		3	1	1	<1
Gastropoda (slugs & snails)		1	15	1	6
Crustacea					
Isopoda (woodlice)		4	18	4	2
Amphipoda (sandhoppers)		2	19	2	5
Myriapoda					
Chilopoda (centipedes)		2	4	-	-
Diplopoda (millipedes)		3	24	2	9
Arachnida					
Acari (mites)	Cryptostigmata	56	1374	49	928
	Pro/Mesostigmata	52	1031	46	1202
	Ixodidae	1	1	1	4
Araneae (spiders)		19	19	13	22
Opiliones (harvestmen)		-	-	1	1
Pseudoscorpionida		1	<1	-	-
Insecta					
Thysanura (silverfish)		1	<1	1	2
Coleoptera (beetles)		32	343	25	209
larvae		15	16	11	18
Collembola (springtails)		67	2041	49	898
Orthoptera (grasshoppers, crickets)		2	5	3	2
Dictyoptera (cockroaches)		1	9	1	6
Diptera (flies & midges)	Brachycera	6	11	7	7
	Larvae	10	41	6	9
	Nematocera	20	180	19	85
	Larvae	6	42	4	6
Heteroptera (bugs)		9	44	5	5
Homoptera (cicadas)		8	31	6	21
Hymenoptera	Formicidae (ants)	1	<1	1	1
	Others (bees, wasps)	17	202	16	143
Lepidoptera (butterflies, moths)		5	9	7	7
Larvae		5	27	6	15
Psocoptera (booklice)		1	7	1	7
Thysanoptera (thrips)		3	11	2	16
Various		8	13	7	13
Totals		361	5548	297	3649

the Mor profiles are high, particularly in the B-horizons, whereas no gravel was found in the WMull profile. This, and the intermediate textural character of the B-horizons of the PMull profile, suggest a gradually advanced stage of weathering in the Mor to WMull sequence. Fresh hard rock was not encountered within the first 300 *cm* in the WMull profile but it occurred at 35–70 *cm* in the

Mor profiles and at *c.* 80 *cm* in the PMull profile (Appendix A). Bulk density (BD) of the mineral soil increased with depth at all four sites, particularly below the Ah-horizon of the Mull soils. Bulk density values in the Mor profile were rather high throughout. Not surprisingly, the porosity values listed in Table 2.8 were inversely related to bulk density ($r^2 = 0.93$, $n = 16$) although the spatial variability in BD (typical standard deviation: 10–20 %) was more pronounced than that of porosity ($\leq$5 %). Saturated hydraulic conductivity (K_{sat}) values were also inversely related to BD, although less pronounced than in the case of porosity ($r^2 = 0.22$, $P < 0.05$, $n = 16$). Generally, K_{sat} decreased rapidly below the Ah-horizon (less so in the MMor profile), particularly in the Mull soils (Table 2.8). However, none of the soils exhibited characteristics of restricted drainage such as mottling (with the exception of a small section of the B-horizon of the WMull profile; Appendix A).

The water holding capacity (WHC, expressed as a fraction of the soil volume) increased below the Ah horizon in the Mor soils but decreased with depth in the WMull soil (Table 2.8). Overall averages were somewhat higher in the MMor and PMull profiles (*c.* 0.35 %) than in the Mor and WMull (*c.* 0.30 %) but spatial variability was large (10–30 % around the mean). The WHC data given in Table 2.8 were used to compute amounts of plant available water (PAW, *mm*) in the top 50 *cm* of the respective profiles (excluding fresh litter, *i.e.* starting at the ectorganic F+H horizons for which an average WHC-value of 24 % was assumed; *Kapos and Tanner* [1985]). A depth of 50 *cm* was used because it contains the bulk of the roots (Appendix A). The resulting PAW totals were 166 *mm* (WMull), 190 *mm* (PMull), 128 *mm* (MMor) and 137 *mm* (Mor). As such, there appears to be a tendency towards higher PAW values for the deeper Mull-type soils compared to the shallower Mor-type soils, but no real trend of decreasing PAW with decreasing forest stature. The Mull-type ectorganic layers contained <10 *mm* of water (6 % of total PAW) *vs.* 65–84 *mm* (51–61 %) in the F+H layers of the Mor-type plots.

Soil chemical characteristics, solid phase

Total (as opposed to extractable) element concentrations in the WMull–Mor soil sequence are listed in Table 2.9. Concentrations of most elements in (relatively) fresh rock material taken in December 1994 from the BC horizons of the PMull and MMor soil profiles were rather similar, with the exception of K_2O (2.6 times higher in the PMull), and CaO (2.8 times lower in PMull), suggesting that the two soils may have developed in near-similar parent material. However, given the fact that the samples were not collected *in situ*, these results must be treated with caution. Despite the possibly different original K_2O and CaO contents of the rocks in the PMull and MMor sites (and possibly the WMull and Mor as well), total concentrations higher up in the profile were very similar in all four plots, suggesting that weathering has advanced sufficiently in all cases to even out initial differences. Yet, the higher concentrations of TiO_2 in the PMull soil might indicate a more advanced weathering stage compared to the other three soils [*Mohr et al.*, 1972]. Mg and Na, but not Ca (similar in all mineral soils), appear to be lower in the Mull-type profiles whereas total P and K levels were

Table 2.8: Variations with depth of: soil texture (clay<2 $\mu m \leq$silt$\leq$63 $\mu m <$sand$\leq 2mm <$gravel), bulk density (BD, $g\,cm^{-3}$), saturated hydraulic conductivity (K_{sat}, $m\,d^{-1}$), porosity ($cm^3\,cm^{-3}$), volumetric water content (θ, $cm^3\,cm^{-3}$) at soil water tensions of -10 *kPa* (pF = 2, 'field capacity') and -1.58 *MPa* ($pF = 4.2$, 'permanent wilting point') and water holding capacity (WHC; $\theta_{pF2} - \theta_{pF4.2}$, $cm^3\,cm^{-3}$) at the WMull, PMull, MMor and Mor forest sites.

Forest	Horizon	Depth	Clay	Silt	Sand	Gravel	BD	K_{sat}	Porosity	θ_{pF2}	$\theta_{pF4.2}$	WHC
		[*cm*]		[% volume]			[$g\,cm^{-3}$]	[$m\,d^{-1}$]			[$cm^3\,cm^{-3}$]	
WMull	Ah	0–14	18.1	38.6	43.3	-	0.61	19.9	0.72	0.702	0.312	0.390
	Bh	14–30	26.7	58.7	14.6	-	0.89	3.58	0.64	0.604	0.237	0.367
	B1	30–56	27.9	37.2	34.9	-	1.06	0.75	0.58	0.564	0.297	0.269
	B2	56–89	40.4	38.8	20.8	-	1.10	0.21	0.57	0.542	0.324	0.218
PMull	Ah	0–14	28.7	40.3	31.0	-	0.44	13.8	0.79	0.455	0.099	0.356
	Bh	14–38	22.6	21.9	53.8	1.7	0.84	0.23	0.68	0.523	0.190	0.333
	Bw1	38–65	7.3	6.7	46.0	40.0	0.98	0.24	0.64	0.512	0.160	0.352
	Bw2	65–82	18.6	20.2	49.1	12.1	1.07	0.01	0.61	0.552	0.180	0.372
MMor	Ah	0–5	21.4	24.0	51.3	3.3	0.39	89.9	0.78	0.369	0.109	0.260
	Bh	5–10	6.4	6.0	36.2	44.4	0.54	23.4	0.78	0.399	0.094	0.305
	Bw	10–35	4.1	3.0	48.4	44.5	0.61	13.7	0.75	0.358	0.090	0.268
	BC	35–$\simeq$70	5.2	4.1	51.2	39.5	0.81	1.4	0.63	0.411	0.087	0.324
Mor	Ah	0–9	28.6	30.0	38.2	3.2	0.72	38.7	0.69	0.638	0.312	0.326
	Bhw	9–19	14.5	14.8	55.1	15.6	0.77	7.04	0.69	0.635	0.237	0.398
	Bw	19–54	6.0	6.4	45.5	42.1	0.76	5.13	0.68	0.663	0.297	0.366
	BC	54–70	10.3	10.6	72.8	6.3	0.89	2.47	0.65	0.634	0.295	0.359

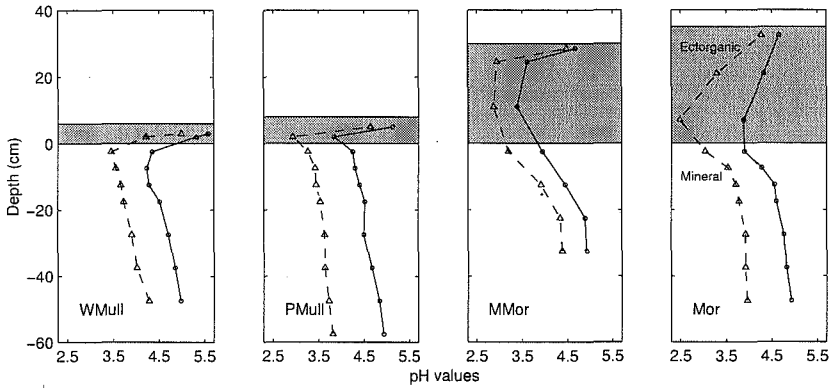

Figure 2.7: Depth profiles of pH_{H_2O} (circles) and pH_{CaCl_2} (triangles) in WMull, PMull, MMor, and Mor forest ectorganic layers (grey sections) and mineral soils; the top of the Ah horizon is taken as the reference depth.

higher in the mineral soil of the MMor plot.

The total concentrations of SiO_2, Al, and Fe in the F+H layers of the PMull profile were much higher than in the ectorganic layers of the MMor (Table 2.9), reflecting the mixing of mineral and organic soil material in the former as well as contrasts in litter chemistry regarding these elements. As will be shown in Chapter 7, Al concentrations in PMull leaf litterfall were three times those of freshly fallen leaves in the MMor.

Concentrations of C and N were distinctly higher throughout the Mor and MMor profiles than in the Mull-type soils. Concentrations of C in the ectorganic horizon of the WMull and Mor profiles were 274 and 527 $mg\,g^{-1}$, *vs.* 15.5 and 19.8 $mg\,g^{-1}$ for total N. The C/N ratios were generally between 16 and 19, except in the Ah and Bh horizons of the WMull (*c.* 12; Table 2.9). The latter may reflect a more advanced humification of WMull-type organic matter compared to the more recalcitrant Mor material.

The variation in pH_{H_2O} and pH_{CaCl_2} with depth is shown in Fig. 2.7. It becomes readily apparent that the largest differences between the respective forests are found in the ectorganic layers where pH_{H_2O} increased from 4.7 in Mor and MMor litter to 5.1 in the PMull litter and 5.7 in WMull litter. Minimum values of both pH_{H_2O} and pH_{CaCl_2} occurred invariably in the H–Ah horizons, although at gradually greater depth in the Mor-WMull sequence (Fig. 2.7). The minimum values for pH_{CaCl_2} (2.5, 2.6, 3.0, and 3.5 for, successively, the Mor, MMor, PMull, and WMull; $n = 13$) differed significantly from each other ($P < 0.01$). Conversely, the pH_{CaCl_2} in the mineral soil increased gradually with depth to *c.* 5.0 at all sites (Fig. 2.7). The contrast between pH_{H_2O} and pH_{CaCl_2} reaches 2.0 pH units in Mor humus but typically amounts to 0.6–1.0 pH units in the mineral soil, illustrating the importance of protons on the exchange complex [*Bolt*, 1976] (see also below).

Table 2.10 summarizes the concentrations of $BaCl_2$-extractable elements and

Table 2.9: Bulk chemical composition of single samples from soil horizons and parent rock underlying the WMull, PMull, MMor, and MMor forests. LOD is the loss on dry-ashing (for 2 h at 500 $^{\circ}C$).

Forest	Horizon	SiO_2	Al_2O_3	Fe_2O_3	MgO	K_2O	Na_2O	CaO	TiO_2	MnO	P_2O_5	LOD	Total C	Total N	C/N
								[all in $mg\,g^{-1}$]							-
WMull	Ah	618	89	36.1	1.92	2.94	0.51	1.21	7.17	0.21	1.04	241.5	100.7	8.13	12.4
	Bh	788	75	40.8	1.30	1.99	0.50	0.30	8.90	0.20	0.51	82.0	25.2	2.17	11.6
	B1	671	160	61	2.93	3.28	0.50	0.40	6.86	0.19	0.46	92.9	12.7	0.74	17.2
	B2-3	515	255	82.3	11.38	5.59	0.78	0.68	8.66	1.24	0.88	118.7	9.3	0.56	16.2
PMull	F+H	224	21	27.5	2.00	1.78	0.70	3.35	6.68	0.32	0.99	711.5	362.4	10.55	34.4
	Ah	590	40	64.1	2.00	2.60	1.30	0.38	17.44	0.21	0.89	280.7	133.4	6.96	19.2
	Bh	691	53	92.9	2.35	3.26	1.33	0.39	20.71	0.27	0.73	134.7	15.5	0.96	16.1
	Bw1	602	136	155.0	7.53	8.29	1.75	0.23	19.39	0.51	0.62	68.1	5.6	0.34	16.5
	Bw2	463	251	137.8	15.64	13.40	1.62	0.14	12.56	1.52	0.65	103.1	9.2	0.52	17.7
	rock	551	161	134.2	55.62	10.42	11.38	1.10	11.14	2.53	0.84	60.9	-	-	-
MMor	F+H	22	7.8	3.9	2.25	1.30	0.25	2.00	0.51	117.18	1.36	956.9	497.7	14.81	33.6
	Ah	249	86	57.5	0.47	2.61	1.23	0.39	6.62	0.16	2.58	593.3	266.2	14.54	18.3
	Bh	388	171	103.9	11.46	5.62	2.31	0.21	9.84	0.46	2.05	304.8	117.8	6.91	17.0
	Bw	448	249	110.6	29.55	12.64	3.97	0.32	9.70	1.36	1.36	133.7	30.3	1.75	17.3
	BC	549	222	94.3	33.20	24.10	3.31	0.16	8.76	2.17	1.12	61.0	6.3	0.37	17.0
	rock	544	200	101.5	48.61	26.33	10.2	0.39	8.29	1.43	0.95	58.4	-	-	-
Mor	Ah	575	109	57.8	8.94	3.97	1.36	0.58	8.46	0.02	0.94	233.3	109.3	5.84	18.7
	Bhw	570	213	54.4	21.47	3.99	1.33	2.15	5.72	0.04	0.66	126.8	27.0	1.74	15.5
	Bw	564	223	46.1	20.14	9.10	3.17	0.20	5.01	0.05	0.62	127.8	25.1	1.65	15.2
	BC	588	218	52.0	25.34	5.11	2.15	0.20	5.52	0.05	0.51	103.2	14.3	1.04	13.8

ammonium oxalate-extractable phosphorus in the four soils. Because of their limited thickness (Appendix A), the F- and H-horizons of the PMull and WMull soils were not analyzed separately. The data in Table 2.10 are generally based on a single sample and therefore the results are only indicative. Turning to the ectorganic layers first, the sum of extractable bases (K^++Na^++Ca^{2+}+Mg^{2+}) in the LFH complex is comparable for WMull, PMull, and Mor material but distinctly lower in the case of the MMor, especially for Ca^{2+}. Overall, extractable Ca, Mg, and K tend to be somewhat higher in Mull-type ectorganics compared to Mor material whereas extractable Al is (much) higher in Mor-type humus.

Similarly, whilst concentrations of Ca, Mg, and K decrease rapidly with depth in Mor-type ectorganic horizons (notably from the F-layer to the H-layer), concentrations of extractable Al and Fe, as well as exchangeable acidity (EA) increase (Table 2.10). Values of the effective cation exchange capacity (ECEC, being the sum of total base cations and exchangeable acidity) of the respective LFH-complexes follow the trends observed for base cations (*i.e.* lowest in the MMor and decreasing towards the humic horizon). This reflects the high base saturation percentages of the ectorganic layers (up to 90 % in Mull F+H material and Mor litter). Aluminium saturation percentages are low in Mull-type ectorganics (<5 %) but attain substantial values in Mor and MMor humic material (20 and 48 %, respectively; Table 2.10).

Differences in ammonium oxalate-extractable P between plots are small although a (single) high value was obtained for the F+H material in the PMull. Most of the differences found for the ectorganic layers of the respective sites disappear upon entering the mineral horizons. The sum of extractable bases is similar for all four topsoils (Ah-horizons) and lowest in the subsoil of the WMull plot, which also has the lowest ECEC. Interestingly, oxalate-extractable P levels are higher throughout the two Mor profiles. Base saturation values in the mineral soil horizons are very low (often <5 %) except in the subsoils of the Mor and MMor plots (16–26 %) and, to a lesser extent, in the WMull profile (9–11 %). The exchange complex in the mineral horizons is dominated by Al, especially in the Mor, MMor, and PMull soils (typically 70–86 %), followed by ammonium (12–36 % in Mor, MMor, and WMull but <10 % in the PMull).

The effective CECs and organic matter percentages (Table 2.10) of the mineral horizons show a strong exponential relationship (coefficients of determination for the WMull, PMull, MMor, and Mor soils 0.81, 0.78, 0.98, and 0.98, respectively; *Spijkerman* [1996]), suggesting that organic matter contributes significantly to (if not dominates) the overall exchange capacity. Such observations are in line with the relatively high clay content of the subsoils (Table 2.8) and the relatively low organic matter content of the WMull soil compared to the other sites (Table 2.9).

A first approximation of the amounts of $BaCl_2$-extractable bases, aluminium and ammonium, oxalate-extractable phosphorus and total amounts of carbon and nitrogen contained in the top 50 *cm* of the four soil profiles (as measured from the top of the F+H ectorganic horizons; *cf.* section 2.3.3) is given in Table 2.11. Some interesting patterns emerge. Amounts of bases are much higher in the Mor soil column (Mor$\gg$PMull$\simeq$WMull>MMor). Furthermore,

Table 2.10: $BaCl_2$-extractable cations, exchangeable acidity, effective cation exchange capacity (ECEC = $\sum$base cations plus exchangeable acidity), base saturation percentage (BSP), aluminium saturation percentage (AlSP), ammonium-oxalate extractable phosphorus ($P_{oxalate}$), and organic matter (OM, %) of ectorganic (litter L, fragmented litter F, and humus H)- and mineral soil horizons in the Mor, MMor, PMull, and WMull forests. All concentrations given in $mmol_c$ per 100 g sample unless indicated otherwise. Samples for ectorganics, Ah and Bh are singles; Bw1–2 are averages of two samples; B1–3 values are averages of four samples. Adapted from *Spijkerman* [1996].

Forest	Hor.	pH_{H_2O}	pH_{CaCl_2}	K^+	Na^+	Ca^{2+}	Mg^{2+}	NH_4^+	Mn^{2+}	Al^{3+}	Fe^{2+}	$\sum$bases	$\sum$cat	EA	ECEC	BSP	AlSP	$P_{oxalate}$	OM
								[all in $mmol_c 100\,g^{-1}$]								[%]	[%]		[%]
WMull	L	5.58	4.99	4.6	0.61	30.7	18.9	-	2.1	0.5	0.00	54.8	57.5	2.2	57.0	96.2	0.9	40.6	-
	F+H	5.32	4.21	3.1	0.64	25.1	13.1	9.5	2.1	2.3	0.10	41.9	55.9	4.8	46.7	89.7	4.9	40.3	-
	Ah	4.35	3.45	0.10	0.05	0.20	0.29	1.3	0.01	3.3	0.02	0.64	5.2	5.3	5.9	10.8	55.2	0.8	12.7
	Bh	4.23	3.55	0.02	0.03	0.05	0.06	0.6	0.00	1.2	0.00	0.16	2.0	1.5	1.7	9.4	72.5	0.5	10.5
	B1-3	4.5-5.0	3.7-4.3	0.04	0.03	0.03	0.04	0.5	0.00	1.0	0.00	0.14	1.7	1.4	1.6	8.5	66.2	0.2	7.8
PMull	L	5.13	4.64	3.3	1.3	32.7	17.2	3.4	2.0	0.3	0.03	54.5	60.1	4.0	58.5	93.1	0.4	-	-
	F+H	3.84	2.93	2.2	0.49	30.4	9.7	7.1	2.4	1.2	0.12	52.8	53.6	4.9	47.6	89.8	2.4	83.9	-
	Ah	4.25	3.26	0.18	0.09	0.12	0.28	1.4	0.01	12.9	0.00	0.67	15.0	14.4	15.0	4.5	85.9	0.7	17.1
	Bh	4.30	3.42	0.04	0.06	0.04	0.08	0.4	0.00	6.4	0.00	0.22	7.1	9.0	9.3	2.4	69.7	0.6	7.6
	Bw1-2	4.4-4.9	3.4-3.8	0.05	0.08	0.14	0.08	0.5	0.00	3.6	0.00	0.35	4.4	4.1	4.4	7.9	80.7	0.4	6.2
MMor	L	4.68	4.48	1.4	0.61	22.8	10.18	3.3	1.4	1.3	0.00	35.0	41.0	4.2	39.2	89.2	3.4	29.6	-
	F	3.62	2.94	1.4	0.79	4.9	8.67	-	0.2	4.6	0.75	15.8	21.3	16.9	32.6	48.3	14.2	47.5	-
	H	3.38	2.86	0.67	0.61	0.8	3.18	5.7	0.05	13.1	2.93	5.2	26.9	21.7	26.9	19.4	48.5	57.5	-
	Ah	3.94	3.19	0.15	0.16	0.17	0.22	3.3	0.00	23.7	0.06	0.70	27.7	27.0	27.7	2.5	85.5	2.4	30.1
	Bh	4.45	3.91	0.04	0.11	0.22	0.09	1.4	0.00	8.2	0.01	0.46	10.1	9.0	9.4	5.0	86.5	1.5	20.1
	Bw	4.91	4.36	0.03	0.12	0.24	0.07	0.5	0.00	1.4	0.01	0.46	2.4	1.4	1.8	25.9	75.7	1.0	11.4
Mor	L	4.66	4.28	1.4	1.1	33.5	14.3	-	0.79	0.3	0.00	50.2	51.2	4.4	54.6	91.9	0.5	20.4	-
	F	4.33	3.30	2.1	1.6	26.3	12.9	5.6	0.38	0.6	0.00	43.0	49.6	8.7	51.7	83.1	1.2	37.9	-
	H	3.88	2.48	1.3	1.3	2.1	9.7	9.9	0.02	6.5	0.66	14.4	31.5	19.7	34.1	42.2	19.2	40.9	-
	Ah	3.90	3.04	0.09	0.08	0.13	0.22	2.8	0.00	10.0	0.01	0.52	13.3	11.7	12.2	4.3	81.8	1.3	18.8
	Bh	4.56	3.71	0.02	0.10	0.11	0.07	0.7	0.00	3.0	0.01	0.30	4.1	3.6	3.9	7.9	77.9	1.0	10.4
	Bw	4.6-4.9	3.8-4.0	0.03	0.15	0.15	0.04	0.8	0.00	1.6	0.01	0.37	2.7	2.0	2.3	15.8	67.1	0.8	7.3

Table 2.11: Amounts of $BaCl_2$-extractable base cations ($kg\,ha^{-1}$), oxalate-extractable phosphorus, total carbon and total nitrogen ($t\,ha^{-1}$) in the upper 50 cm of the soil column in the Mor, MMor, PMull and WMull forests starting from the ectorganic F+H horizon. Computations are based on the bulk density values listed in Table 2.8 and the concentrations given in Table 2.9 (total C and N) and Table 2.10 (other elements). An average bulk density of 0.07 $g\,cm^{-3}$ was assumed for the F+H horizons [*Kapos and Tanner*, 1985]).

Forest	K	Na	Ca	Mg	NH_4	Mn	Al	Fe	P	C	N
	[all in $kg\,ha^{-1}$]								[all in $t\,ha^{-1}$]		
WMull	98	31	199	93	415	21	553	4	0.84	146.2	11.32
PMull	112	58	227	82	321	23	2154	1	1.31	129.7	6.87
MMor	86	65	115	111	349	5	908	93	3.77	201.8	8.89
Mor	199	107	844	368	553	17	775	14	3.37	205.1	8.22

amounts of oxalate-extractable P are 3 to 4 times higher in the Mor and MMor soils whereas the highest amount of total N is obtained for the WMull followed by the MMor forest. No clear trend exists for extractable NH_4^+, but again the highest value is found for the Mor forest. Extractable Al^{3+} is very high in the PMull column, whereas extractable Fe (but not Mn) is very low in the Mull soils. Although it remains to be seen how much of the total N and oxalate-extractable P is available to plants (see below and Chapters 7, 9), the data in Table 2.11 do not support the view that the soils underlying stunted Mor-type forest have a lower nutrient pool than forests on Mull soils.

Soil chemical characteristics, liquid phase

Average monthly chemical concentrations in litter percolate and soil water extracted at various depths from the four plots between December 1995 and April 1996 ($n = 5$) are listed in Table 2.12. Although 19 sample sets were retrieved from the PMull and MMor sites over a 16-month period, the present comparison is restricted to the five months for which corresponding data are available for the Mor and WMull sites as well.

The pH in both litter percolate and soil water paralleled the trends observed for the pH_{H_2O} of the soils (Fig. 2.7): minimum values occurred in the Ah-horizons of all four sites, with those for the Mor and MMor sites being low enough to fall in the aluminium buffer range [*Khanna and Ulrich*, 1984]. Also, the pH generally increased again with depth in the mineral soil. The concentrations of Na^+, Ca^{2+}, Mg^{2+} and K^+ in litter percolate (LP) mirrored those of BaCl-extractable bases in the LFH-complex in that values in the MMor plot were again the lowest of all. Concentrations of base cations in the litter percolate from the Mor plot were remarkably high but decreased rapidly upon entering the mineral soil where concentrations became similar to those in the MMor and PMull plots and, generally, well below those in the WMull. It is possible, however, that the high solute concentrations in the litter percolate from the Mor are an artefact caused by placing back too much leaf litter on the percolation plates upon installation.

Table 2.12: Field pH, base cations, total aluminium, nitrogen and phosphorus species, sulphate and dissolved organic carbon (DOC) and total polyphenols in litter percolate (LP) and soil moisture extractions from selected horizons in the WMull, PMull, MMor, and Mor forests. Apparent values for dissolved organic nitrogen (DON) and phosphorus (DOP) were derived by subtracting mineral species concentrations from concentrations of total N. MMor and PMull data are averages of five extractions (December 1995–April 1996; see text); Values for WMull, Mor, DOC and total phenols (both in $mg\,l^{-1}$) represent averages of three samples only.

Site	Horizon	pH	Na	K	Mg	Ca	$\sum$bases	Al	NH_4	NO_3	N_{tot}	DON	PO_4	P_{tot}	DOP	SO_4	DOC	Phenols
			[all in $\mu mol\,l^{-1}$]									[all in $\mu mol\,l^{-1}$]					[$mg\,l^{-1}$]	[mg TAE l^{-1}]
WMull	LP	5.34	84.1	142.7	68.8	106.5	402.1	8.8	74.2	177.7	183.6	-68.3	0.33	3.25	2.92	55.5	18.6	2.8
	Ah	4.98	61.3	45.5	54.5	38.7	200.0	18.9	71.3	94.8	67.1	-38.9	0.45	0.67	0.22	32.7	12.0	2.7
	Bh	5.24	99.2	50.7	27.6	21.9	199.2	5.8	7.6	68.0	41.1	-34.5	0.52	0.98	0.46	18.6	8.0	0.7
	B13	5.45	63.9	12.3	22.8	16.2	115.3	1.8	5.0	31.4	44.8	8.4	0.34	0.48	0.12	6.7	7.2	0.4
PMull	LP	5.51	72.4	77.9	49.9	68.5	268.7	7.6	8.8	7.9	61.7	44.9	0.11	1.29	1.18	44.7	21.2	2.9
	Ah	4.82	66.6	10.3	20.7	10.6	108.1	20.8	10.6	7.9	50.4	31.8	0.13	0.69	0.56	12.4	13.0	1.6
	Bh	5.01	34.9	4.2	14.0	6.9	60.0	7.8	5.6	1.8	28.9	21.5	0.10	0.46	0.37	3.2	7.4	0.7
	Bw12	5.32	52.4	7.3	15.8	7.2	82.7	2.9	4.2	7.7	22.1	10.2	0.20	0.61	0.41	11.6	5.8	0.5
MMor	LP	5.58	59.5	48.2	37.1	43.0	187.9	2.3	4.7	2.0	62.8	56.1	0.10	1.14	1.04	29.1	15.9	3.6
	Ah	4.10	56.4	9.4	24.5	11.5	101.7	42.6	8.3	6.3	47.5	32.9	0.10	0.95	0.84	65.2	20.1	5.0
	Bh	4.53	41.7	8.2	16.5	2.4	68.8	18.8	6.9	12.5	26.1	6.7	0.12	0.58	0.46	10.7	11.4	1.2
	Bw	5.24	50.4	6.5	12.3	3.2	72.5	11.1	8.8	3.7	30.4	18.0	0.10	0.57	0.47	9.3	9.0	0.6
Mor	LP	4.64	106.1	89.4	96.2	137.1	428.8	2.4	23.7	2.2	151.3	125.3	0.18	2.04	1.86	138.0	63.7	11.5
	Ah	3.89	50.6	16.5	39.4	14.4	120.9	58.4	8.2	4.4	59.0	46.4	0.26	0.99	0.73	115.3	43.5	7.8
	Bhw	5.06	42.6	4.7	13.5	6.7	67.5	12.4	7.3	2.0	30.4	21.0	0.27	0.50	0.23	10.1	11.8	0.6
	Bw	4.87	43.4	5.0	13.8	7.0	69.2	2.6	8.4	18.4	51.5	24.7	0.31	1.17	0.86	17.8	7.5	0.3

The generally observed decreases in base cation concentrations in soil water with depth were least pronounced in the WMull. Base cations ranked in the order WMull$\gg$Mor$\geq$MMor$\simeq$PMull and thus did not reflect the trends in pH and forest stature (both decreasing from WMull to Mor). On the other hand, concentrations of NO_3^-, were highest throughout the WMull profile (including litter percolate) and relatively low at the other sites. Concentrations of NH_4^+ in soil water were comparable among the four sites (although NH_4^+ levels in the litter percolate of the WMull and, to a lesser extent, in the Mor were also elevated). Therefore, total mineral nitrogen ($NH_4^+ + NO_3^-$) concentrations in soil water were highest in the WMull and much lower (but comparable) for the other plots. As a result of the high NO_3^- concentrations in the WMull soil, apparent DON values (*i.e.* total N minus mineral N) became negative, suggesting serious underestimation of concentrations of total N in the WMull (if not in the other sites). Differences in concentrations of total phosphorus and apparent DOP (total P minus phosphate-P) between soils were small whereas ortho-phosphate concentrations rank in the order WMull>Mor>PMull$\simeq$MMor, *i.e.* similar to the ranking observed for base cations (Table 2.12). Patterns for sulphate did not show a clear trend between forests but the highest concentrations in the litter percolate (Mor site) were matched by maximum values for Mg and Na as well, possibly suggesting a maritime influence.

Concentrations of dissolved organic carbon (DOC) were progressively reduced in the Mor–WMull sequence, showing the strongest contrasts between sites in the Ah-horizon and smaller differences in the litter percolate. A similar trend was observed for phenolic compounds which, on average, made up about 19 % of total DOC (Table 2.12). Concentrations of total phenols showed a good correlation with DOC values, regardless of the origin of the samples ($r^2 = 0.92$, $n = 48$; Fig. 2.8). Absolute concentrations of phenols in Mor and MMor topsoils were about twice those in Mull topsoils (Table 2.12). Lower down in the profiles (Bw horizons and downwards) DOC values and inter-site differences were reduced, as were concentrations of phenols and the degree of correlation between the latter and DOC ($r^2 = 0.33$, $n = 24$, $P < 0.05$).

Finally, patterns of total Al concentrations reflect those observed for pH, *i.e.* values we re highest where pH is low and *vice versa.* Maximum values of total Al were observed in the Ah-horizons of the Mor and MMor soils but these were not paralleled by high concentrations in the litter percolate. Interestingly, Al concentrations in the litter percolate (but not in soil water) from the two Mull sites were about three times higher than in the two Mor forests. Concentrations of iron and manganese (not shown in Table 2.12) hardly exceeded the respective detection limits (0.9 $\mu mol\, l^{-1}$), except for Fe in soil water from the Ah-horizon (16.0, 12.6 and 4.0 $\mu mol\, l^{-1}$ in the Mor, MMor, and PMull, respectively).

In view of the high concentrations of total aluminium observed in the moisture extracted from (especially) the Ah-horizon in the Mor and MMor profiles (Table 2.12), thermodynamical computations using the adjusted PHREEQC model [*Parkhurst*, 1995; *Driscoll and Schecher*, 1988] were carried out to examine whether potentially toxic concentrations of free Al^{3+} (plus $Al(OH)_1^{2+}$ and $Al(OH)_2^+$; *Kinraide and Parker* [1990]; *Kinraide* [1991]) might occur. The

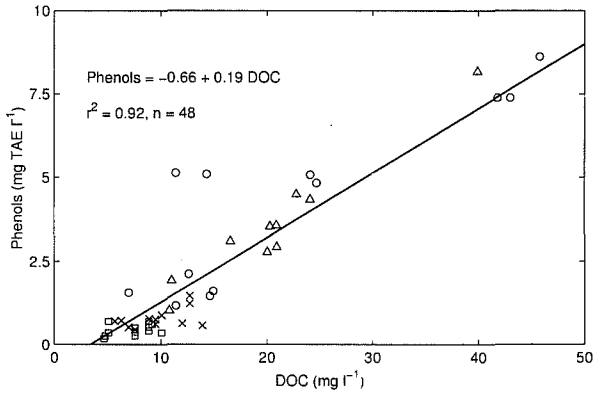

Figure 2.8: Relationship between concentrations of dissolved organic carbon (DOC, $mg\,l^{-1}$) and total phenols ($mg\,\mathrm{TAE}\,l^{-1}$) in litter percolate (△) and soil moisture from the Ah (○), Bh (×), and BC (□) horizons of the four forest sites.

calculations suggested typical concentrations of free Al^{3+} of 15–20 $\mu mol\,l^{-1}$ in the Mor-type Ah-horizon *vs.* 1.1–1.5 $\mu mol\,l^{-1}$ in the PMull and WMull (Fig. 2.9). Augmentation of Al^{3+} concentrations with those of the mono-nuclear Al-hydroxy species $Al(OH)_2^+$ and $Al(OH)_1^{2+}$ (the species $Al(OH)_3^0$ and $Al(OH)_4^-$ were not present in significant concentrations under the prevailing pH conditions; *Kinraide and Parker* [1990]; *Kinraide* [1991]) roughly doubled the potential Al-toxicity in the Mull-type Ah-horizons but had limited effect in the case of the Mor soils (+1 $\mu mol\,l^{-1}$).

The speciation calculations indicate that a considerable portion of the total Al present in litter percolate and soil water is complexed by aqueous organic material (grey sections in Fig. 2.9). Estimates range from 60 % in the water extracted from the Ah-horizon of the MMor plot to 95 % in litter percolate from the MMor and Mor forests (Fig. 2.9). Minerally complexed Al (notably by SO_3^- and 1,2-hydroxy groups) amount to *c.* 10 % of the total Al present in soil-water extracted from subsoil horizons and to *c.* 5 % in the litter leachate from the PMull and WMull forests (Fig. 2.9). The potential influence of the presence of such strong complexing mineral ligands like fluoride [*Driscoll and Schecher*, 1988] was modelled using an assumed concentration of 2 $\mu mol\,l^{-1}$ of F and the stability constants for the respective Al-F complexes given by *Driscoll and Schecher* [1988]. The inclusion of fluoride in the speciation calculations reduced the predicted concentrations of free Al^{3+} in litter percolate by 9–27 % and in subsoil moisture by 17–62 %. However, the corresponding reduction obtained for Al^{3+} concentrations in soil water from the Ah horizons in the Mor-type soils was only 4–6 % and concentrations therefore remained high (14–19 $\mu mol\,l^{-1}$).

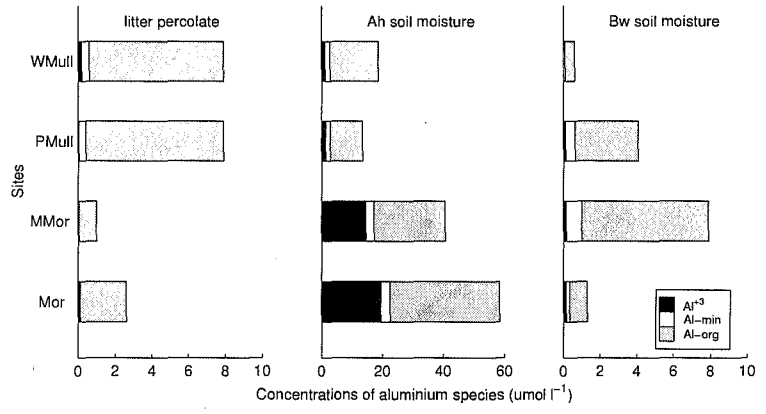

Figure 2.9: Speciation of total aluminium in selected samples of litter percolate and soil moisture ($n = 3$) as calculated with PHREEQC [*Parkhurst*, 1995]. Note that the values on the X-axis for soil moisture from the Ah-horizon are six times those for the other sample types. Al^{3+} is presented by the black sections. Al-min (white sections) is labile, minerally-complexed aluminium; Al-org (grey sections) is non-labile, organically complexed aluminium (see text for details).

2.4 Discussion

2.4.1 Forest structure, floristics and foliar characteristics

On the basis of their average tree height, the number of trees with multiple stems and trunk/tree ratios, the classification of the PMull and MMor forest plots as intermediate forest types within the Mor–Mull–WMull sequence distinguished by *Tanner* [1977a, 1980b] seems justified (Table 2.1). However, the ranking of the MMor forest as being intermediate between the PMull and the Mor forest could be questioned in view of its low basal area (44.4 m^2ha^{-1} *vs.* 64.7 m^2ha^{-1} in the Mor), high number of trees (6043 ha^{-1} *vs.* 4900 ha^{-1} in the Mor) and low number of species (10 *vs.* 16 in the Mor). To some extent, the low number of species in the MMor is an artefact of the relatively small size of the plot. According to the species-area curve derived by *Tanner* [1977a] for the Mor forest, the size of the MMor plot (0.024 *ha*) would cover *c.* 70 % of the potential species range. As such, the MMor forest could be expected to contain *c.* 14 tree species if the plot size would have been equal to that of Tanner's Mor Ridge plot (0.08 *ha*). The slightly lower species richness, basal area and mean d.b.h. of the MMor forest, coupled with the high stem density and the common occurrence of the introduced species *Cinchona pubescens* in the understorey (Table 2.5), all point to some past natural- or anthropogenic-disturbance and a non-climax character of at least part of the MMor forest area.

The low value derived for the tree leaf area index (LAI) of the PMull forest plot (3.4 *vs.* 4.1 m^2m^{-2} for the MMor–Mor forests and 5.1 m^2m^{-2} for the WMull) on the basis of average SLA and leaf litterfall must be considered an

anomaly. The most likely explanation is that the SLA of the PMull has been underestimated to some degree, given the fact that the annual leaf fall in the PMull (512 $g\,m^{-2}yr^{-1}$; Chapter 8) was intermediate between those in the MMor (462 $g\,m^{-2}yr^{-1}$) and Mull forests (532 $g\,m^{-2}yr^{-1}$; 1974/75; *Tanner* [1980a]). On the basis of light attenuation (PAR) measurements, a value of 5.0 was estimated for the PMull which must be considered more plausible (see Section 4.4.3). The generally reported reduction in specific leaf area (SLA) with increasing elevation on tropical mountains (*i.e.* decreasing forest stature) [*Grubb*, 1974; *Körner et al.*, 1983] is basically absent in the PMull–MMor–Mor sequence, although a distinctly higher average value was found for the WMull (Table 2.1; *cf.* Table 2.4). No significant differences were found between average leaf size, weight and SLA of seven principal tree species in the PMull and MMor plots, but three out of four species showed increased leaf thickness in the MMor ($P < 0.001$; Table 2.4). *Tanner and Kapos* [1982] also did not find any statistically significant differences for a large number of leaf structural characteristics (including SLA) between Mor and Mull forests at *c.* 1600 *m* a.s.l. although the leaves in their Mor forest were also thicker on average. The relatively small contrast in altitude between the MMor (1824 *m* a.s.l.) and the Mor (1600 *m* a.s.l.) is probably responsible for the very similar SLA values of the two forests [*cf. Bruijnzeel and Veneklaas*, 1998]. The high SLA and LAI of the WMull forest (which is situated at a comparable elevation as the Mor forest) must therefore reflect an edaphic effect [*cf. Loveless*, 1961; *Kapos*, 1982].

2.4.2 Soil biotics

The abundance of fungi in litter (highest in the PMull) is paralleled by the distribution of fungivores and their predators. Not surprisingly, both Collembola (springtails) and Acari (mites) are the most abundant (meso)-faunal groups in both forests which may directly affect the numbers of predators (mainly *Staphylinidae*) among the Coleoptera (beetles) and Chilopoda (centipedes). The contrasting densities of fragmenters (Isopoda, Diplopoda, and Diptera larvae which are all higher in the PMull) are likely to be responsible for the more rapid decay of litter in the taller forest (Table 9.1). Given the relatively large size of Diplopoda (millipedes) compared to other groups, the inter-site contrast would increase significantly if the presence of fragmenters would be expressed in terms of biomass per unit area/weight. The distinct absence of *Isoptera* (termites) and the low values of *Formicidae* (ants) are typical for the majority of tropical forest ecosystems at high elevations [*Janzen*, 1983; *Olson*, 1994]. Hymenoptera (other than ants) and adult Diptera (flies and midgets) were present in considerable numbers in both forests, despite escape possibilities from the litterbags. Apparently, winged adults find ground dwelling conditions favourable enough for their reproduction. Oligochaeta (*e.g.* earthworms), which are important for decomposition and redistribution of organic matter [*Lee*, 1985; *Hendrix*, 1995], were only found in too small numbers to allow for a useful interpretation.

2.4.3 Forest stature and soil water dynamics

The generally high permeability and porosity of the soils underlying the Mor, MMor, PMull, and WMull forests (Table 2.8) and the absence of gleyed horizons (Appendix A) provide ample evidence that the rooted parts of the four soil profiles do not suffer from waterlogging. Further general support for this contention comes from monthly observations of gravimetric soil water contents in the Mor and Mull forests throughout 1980 by *Kapos and Tanner* [1985] and more specifically by the measurements of soil water tension at 3–4 day intervals between January 1995 and April 1996 during the present study (see Chapter 5 for details). As for the sensitivity to drought of the four plots, the amounts of plant available water (PAW) in the top 50 *cm* of the respective soil columns (including ectorganic layers), where >90 % of the fine root mass is found [*Tanner*, 1980b; *Elbers*, 1996], show a moderate difference between Mor-type (PAW 128–137 *mm*) and Mull-type soils (PAW 166–190 *mm*; Table 2.8). These values correspond with average volumetric moisture contents of *c.* 27 % (Mor and MMor) and 33–38 % (PMull and WMull). *Kapos and Tanner* [1985] estimated a topsoil PAW of 23 % for the F-layer in the Mor forest and the Ah-horizon in the Mull forest. As such, there is no consistent trend in PAW that reflects the gradual decrease in stature within the sequence of four forests (*cf.* Table 2.1). By comparison, the top 20 *cm* of the soil underlying a much taller (>30 *m*) montane rain forest at 2300 *m* a.s.l. in Venezuela had a PAW of *c.* 52 *mm* with an additional 35 *mm* in the B-horizon (found between 20 and 45 *cm*; *Steinhardt* [1979]), *i.e.* much lower than the presently found totals. In addition, annual rainfall at the Venezuelan site is distinctly lower than that in the study area (1760 *vs.* 2850 *mm*). Neither *Kapos and Tanner* [1985] in the Mor and Mull forests at 1600 *m* a.s.l., nor the present study in the PMull and MMor forests (Chapter 5) observed critically low soil water levels (*i.e.* $\psi_m \leq -1.58$ *MPa*, or 'permanent wilting point'). Furthermore, a drought sensitivity simulation exercise [*Hafkenscheid et al.*, 1999] suggested that it would take more than 17 weeks without rain for the top 38 *cm* of the PMull mineral soil (Ah+Bh horizons) to reach wilting point *vs.* 6–12 dry weeks in the case of the MMor Ah–Bh horizons. Comparison with the long-term rainfall record at Cinchona Botanical Garden (1500 *m* a.s.l.) showed that such long droughts are very unlikely to happen (*J. R. Healey, personal communication*). In conclusion, the contrasts in stature among the four forest plots do not seem to reflect substantial differences in soil water dynamics.

2.4.4 Forest stature and soil nutrient status

When studying the extent to which the productivity of a forest is constrained by low nutrient availability, investigations usually focus on such relatively easy measurements as nutrient concentrations in foliage, leaf litterfall or soil chemical extracts, rather than take the more time consuming route of forest fertilization experiments [*Tanner et al.*, 1990, 1998]. *Tanner et al.* [1998] recently reviewed the available evidence on nutrient limitation and forest growth on wet tropical

mountains. Briefly, foliar concentrations of N, P, K, Ca, and Mg do not show statistically significant correlations with site elevation (*i.e.* decreasing forest stature) for a large number of sites. Conversely, for forests situated at a single mountain, foliar N decreases with altitude (n = 5 studies), K and P usually decrease (but not invariably so) whereas Ca and Mg do not show any consistent trends. Also, N and P concentrations in (leaf) litterfall are lowest in forests above 1500 m a.s.l. (but not systematically between 1000 and 1500 m). This, together with the reduced rates of litterfall found in montane forests, leads to decreased cycling of especially N and P, and to a lesser extent of K, Ca, and Mg compared to lowland forests [*Grubb*, 1977; *Vitousek*, 1984]. Again, transects on the same mountain invariably show lower concentrations of N in litterfall (n = 4) but usually not of P (3 out of 4 studies) with increasing elevations / reduced stature [*Bruijnzeel and Proctor*, 1995].

For three ridge-top forests of contrasting stature in the present study area (tall Gap forest, intermediate Mull Ridge forest and stunted Mor Ridge forest) *Tanner* [1977a, b] reported gradually decreasing concentrations of N, P, K, and Ca in both living foliage and leaf litterfall, suggesting that all of these elements could increasingly limit forest growth. A comparison of amounts of 'exchangeable' Ca and K (as determined with the NH_4^+-acetate extraction technique at pH = 8) in the top 40–45 *cm* of the soil revealed the same trends, as did amounts of NH_4-N and NO_3-N in the first 10 *cm* [*Tanner*, 1977a]. No data were given for soil P, but later a (heavy) fertilisation with N and P of the intermediate-statured Mull Ridge forest produced significant increases in trunk-diameter growth of 77 % after addition of N and 32 % after addition of P [*Tanner et al.*, 1990]. Recently, root ingrowth experiments using N- and P-enriched perlite cores produced strongly and significantly increased root ingrowth rates for both N and P in the Mor forest (+350 %) but only for N (+286 %) in the Mull forest. A 243 % increase after P-addition in the Mull forest was not significant [*Stewart*, 1999].

In view of the fact that: (i) there does not seem to be a straightforward relationship between tropical forest stature and the pool of ammonium-acetate extractable nutrients in the soil, not even for forests situated on one and the same mountain [*cf. Proctor et al.*, 1983b, 1988; *Grieve et al.*, 1990; *Pendry and Proctor*, 1996a]; (ii) different extraction techniques were used to characterize soil nutrient status of the Mull and Mor Ridge forests by *Tanner* [1977a] and the present study which are known to produce different results [*Haynes and Swift*, 1989; *Amacher et al.*, 1990; *Silver et al.*, 1994]; and (iii) the very limited number of replications for our soil chemical analyses ($n = 1-3$ except for mineral N (n = 13) and pH (n = 13)), the following discussion of the soil chemical characteristics of the four study plots in relation to forest stature largely focuses on hydro-chemical aspects, *i.e.* easily available nutrient elements.

Table 2.13 summarizes the relative rankings of the respective forest plots on the basis of the chemistry of their litter percolate and soil water. Rankings based on $BaCl_2$-extractable cationic concentrations in both ectorganic and Ah-horizons (Table 2.10) have been added for comparison. A number of striking patterns emerge from Table 2.13.

Table 2.13: Relative ranking of the four forest sites on the basis of the chemistry of their litter percolate and soil water, and concentrations of water- and $BaCl_2$-soluble nutrients in their ectorganic (F+H) layers and Ah horizons.

(1)	Forest stature:	WMull	$>$	PMull	$>$	MMor	$\simeq$	Mor
(2)	Litter percolate:							
	Ca, Mg:	Mor	$>$	WMull	$>$	PMull	$>$	MMor
	K, PO_4, NH_4:	WMull	$>$	Mor	$>$	PMull	$>$	MMor
	NO_3:	WMull	$\gg$	PMull	$>$	Mor	$\gtrsim$	MMor
	Al*:	PMull	$\gtrsim$	WMull	$\gg$	Mor	$\gtrsim$	MMor
	pH:	Mor	$<$	WMull	$<$	PMull	$\lesssim$	MMor
(3)	Soil water Ah							
	Ca, Mg:	WMull	$>$	Mor	$>$	MMor	$\gtrsim$	PMull
	K, PO_4:	WMull	$>$	Mor	$>$	PMull	$\gtrsim$	MMor
	NH_4, NO_3, pH:	WMull	$>$	PMull	$>$	MMor	$>$	Mor
	Al:	Mor	$>$	MMor	$>$	WMull	$>$	PMull
(4)	$BaCl_2$-extractable F+H							
	$\sum$ bases:	PMull	$\gtrsim$	WMull	$\gg$	Mor	$>$	MMor
	NH_4:	WMull	$\gtrsim$	Mor	$>$	PMull	$>$	MMor
	Al:	MMor	$>$	Mor	$>$	WMull	$>$	PMull
(5)	$BaCl_2$-extractable Ah							
	Ca+K+Mg:	WMull	$\gtrsim$	PMull	$>$	MMor	$>$	Mor
	NH_4:	MMor	$\gtrsim$	Mor	$>$	PMull	$\gtrsim$	WMull
	Al:	MMor	$>$	PMull	$>$	Mor	$\gtrsim$	WMull

*both total Al and Al^{3+} (*cf.* Fig. 2.9).

First, the ranking of the four plots by stature is mimicked by the concentrations of NO_3^- in litter percolate whereas there is an inverse relationship with concentrations of Al^{3+} (but not pH). If the exceptionally high concentrations of Ca^{2+} and Mg^{2+}, and to a lesser extent K^+, NH_4^+ and PO_4^{3-} in the litter percolate from the Mor are excluded (these possibly being an artefact of an unrepresentative amount of litter above the collection plates), then the sequence WMull>PMull>MMor is reflected in the same relative concentrations of these elements as well. Secondly, concentrations of NO_3^-, NH_4^+ and H^+ in soil water extracted from the Ah-horizons also follows the sequence found for forest stature, with that for Al^{3+} again showing a reverse pattern. However, the concentrations of base cations (K^+, Ca^{2+}, Mg^{2+}), N_{tot}, and PO_4^{3-} in soil water extracted from the Ah-horizon of the 'impoverished' Mor site are such that it ranks second after the WMull for these elements and even ranks first (followed by the MMor) for P_{tot}. Thirdly, concentrations of $BaCl_2$-extractable elements (including Al) do not show clear trends, although the sum of Ca^{2+}, Mg^{2+} and K^+ concentrations in both ectorganic (F+H) horizons and Ah-horizons exhibits a negative trend that more or less follows that of the average canopy height (Table 2.13).

Water- and KCl-extractable amounts of NH_4-N and NO_3-N were determined for the top 15 *cm* of the soils of the PMull and MMor forest plots, whereas *Tanner* [1977a] gave KCl-extractable values for the first 10 *cm* of soil in the Mull and Mor Ridge forest plots. As shown in Table 2.14, the concentrations of NO_3-N obtained by *Tanner* [1977a] and the present study are of the same order of magnitude, although the high value reported for the Mor forest seems improbable in view of the low concentrations observed in the MMor plot and all

other montane forests. Similarly, the concentrations of KCl-extractable NH_4-N in the Mull and Mor forests listed by *Tanner* [1977a] are extremely high, not only in comparison to the values obtained for the MMor forest (which are 2.3 times lower), but also compared to results obtained elsewhere (Table 2.14). These high values of NO_3-N do not suggest excessive leaching of mobile N species, despite the combination of high rainfall (>3000 $mm\,yr^{-1}$) and high permeability of the soils of the study area. However, rainfall in the month prior to the collection of the soil samples was not excessive (<9 $mm\,d^{-1}$on average, *i.e.* similar to the 1995 daily rate). As macropore flow is probably an important component of the infiltration and drainage capacity of these soils [*cf. Beven and Germann*, 1982], high NO_3^- concentrations in more or less stagnant water held in micro-pores may have contributed to the high NO_3^- found in the mineral soil. The high concentrations of NO_3^- in the water extracted from the Jamaican and other montane soils (Table 2.15) seem to support this interpretation.

The relatively high amounts of mineral N found in the Jamaican soils would argue against a shortage of mineral N in, especially, the Mor-type forests as the main causative factor of forest stunting (*cf.* Section 9.3.3), unless the trees would be unable to make full use of the nitrogen [*cf. Bruijnzeel et al.*, 1993]. Further comparative synchronous observations of mineral N in the four plots are desirable.

As shown in Table 2.15, nutrient element concentrations in topsoil moisture of a tall (>30 m) montane forest site in Venezuela [*Steinhardt*, 1979] were well below those in the Ah-horizon of the WMull site and even below those of the Mor site (except for Ca^{2+} and K^+). Similarly, concentrations in soil water at 70 *cm* depth in a Dystric cambisol derived from basaltic volcanic deposits underlying tall colline rain forest in Costa Rica [*Parker*, 1985] had lower Ca^{2+}, K^+, NH_4^+, and PO_4^{3-} than subsoil water extracted from the WMull site, although NO_3^- was higher in Costa Rica. Such comparisons, as well as the relatively high concentrations in soil water in the Mor forest (Table 2.15), suggest that amounts of base cations and P are less important as causative factors for forest stunting in Jamaica. Rather, as also suggested by the gradual decrease in foliar concentrations of P, K, and Ca in the Gap forest ($\simeq$WMull)–Mull–Mor forest sequence [*Tanner*, 1977a], the trees in the more stunted forest types seem to take up less of each element as the soil becomes more acid.

A comparison of the amounts of nutrient elements that are annually supplied via bulk precipitation [*Tanner*, 1977b] with amounts actually taken up for trunk growth [*Tanner*, 1985], shows that the latter constitute only a fraction of the former [*Bruijnzeel*, 1989b]. *Tanner et al.* [1998] suggested that perhaps the concentrations of the extra nutrients in precipitation are too low to be available to plants, but concentrations in crown drip and stemflow, and especially in water in the litter and topsoil complex where most of the nutrient uptake takes place, are generally much higher (*Burghouts* [1993], *Bruijnzeel et al.* [1993]; *cf.* Tables 2.12 and 2.15). Its is more likely, therefore, that the uptake of available nutrients becomes limited somehow in the rooting medium. *Bruijnzeel et al.* [1993] suggested that high concentrations of polyphenols in litter and topsoil could be important in this respect whereas *Tanner* [1977a] proposed that K-

Table 2.14: Concentrations of mineral nitrogen (NO_3-N and NH_4-N, $\mu g\, g^{-1}$) and total nitrogen (%) in topsoil material from tropical montane forests.

Locality	Elevation [m]	Depth [cm]	KCl-extractable N NO_3-N	KCl-extractable N NH_4-N	Water-soluble N NO_3-N	Water-soluble N NH_4-N	Total N [%]	Forest type [-]
Gunung Silam,	680	0–5	-	65.9	2.9	32.3	0.06	tall LMRF
Malaysia[1]	870	0–5	-	43.8	2.66	24.8	0.4	short LMRF
Serrania de Maguira, Colombia[2]	750	0–10	0.38	12.7	-	-	0.24	7–10 m,stunted 'elfin' forest
Volcan Barva,	1000	0–10	4	<5	-	-	1.4	LMRF
Costa Rica[3]	1500	0–10	$\lesssim$4	5	-	-	1.8	LMRF
	2000	0-10	3	7	-	-	1.9	LMRF
	2600	0–10	1.5	17.5	-	-	1.9	LMRF
Blue Mountains,								
Jamaica[4] Mor	1600	0–10	31	364	-	-	1.6 (F)	stunted UMRF
Mull	1600	0–10	17	239	-	-	1.7 (FH,Ah)	intermediate UMRF
Blue Mountains,								
Jamaica[5] Mor	1600	0–9	-	-	16.5	7.2	-	stunted UMRF
MMor	1824	0–5	10	149	17.9	14.4	1.4 (1.5 FH)	stunted UMRF
PMull	1809	0–14	26	102	16.2	13.8	0.7 (1.1 FH)	intermediate UMRF
WMull	1600	0-14	-	-	26.2	61.7	-	intermediate UMRF
Genting, Malaysia[6]	-	0-14	0.1	0.9	-	-	0.28	Dipterocarp 'hill' forest
	-	0–14	0.1	1.3	-	-	0.29	sub-montane
Mauna Loa, Hawaii[7]	1220	0–6	0	18	-	-	1.4	2–4 m, *Metrosideros*
	1585	0–6	0	33	-	-	1.4	2-4 m,*Metrosideros*, closed canopy
Bukit Belalong, Brunei[8]	200	0-5	5.2	-	-	-	0.36	LRF
	520	0–5	6.4	-	-	-	0.46	LRF
	880	0-5	4.8	-	-	-	0.57	LMRF
Gunung Rakata, Indonesia[9]	700	0–5	1.82	30.7	-	-	0.66	stunted 'elfin' forest

[1] *Bruijnzeel et al.* [1993], *Waterloo* [1989]; [2] *Cavelier* [1988]; [3] *Marrs et al.* [1988]; [4] *Tanner* [1977a]; [5] this study; [6] *Chandler* [1985]; [7] *Vitousek et al.* [1988]; [8] *Pendry and Proctor* [1996b]; [9] *Hafkenscheid* [1994].

uptake in the Mor forest might be hampered by high concentrations of H^+. Concentrations of phenols in litter and topsoil water at the Mor forest plot were roughly 2–3 times higher than in the PMull and WMull with intermediate values for the MMor site (Table 2.12). We will return to this point later.

Another marked contrast between the four plots concerns that for 'free' Al^{3+} (as opposed to total Al; Tables 2.12 and 2.16 and Fig. 2.9). Concentrations of Al^{3+} in water extracted from the Ah-horizon in the Mor-type forests (*c.* 15–20 $\mu mol\, l^{-1}$) greatly exceeded those associated with the Mull-type forests (1–1.5 $\mu mol\, l^{-1}$). In their extensive review of the effects of soil aluminium levels on plant growth, *Cronan and Grigal* [1995] considered the molar ratio Ca^{2+}/Al^{3+} in soil solutions to be a useful tool for the distinction between different degrees of aluminium-induced stress. When Ca^{2+}/Al^{3+} fell below 1.0, there was an adverse effect on tree growth in 50 % of the examined studies. For Ca^{2+}/Al^{3+} $\leq$0.1 this figure even rose to 90 % [*Cronan and Grigal*, 1995].

Values for Ca^{2+}/Al^{3+} in the water extracted from the Mor-type Ah-horizons of the study plots were typically <0.75 (with $Ca^{2+}/H^+ \simeq 0.1$) whereas corresponding values in the Mull-type Ah-horizons were 4.2–32.5, respectively (Table 2.16). In short, these various indications of potential Al-toxicity reveal a pattern for the four study sites that is more consistent with forest physiognomy than that based on pools of base cations, P, and perhaps even mineral N (Tables 2.12, 2.13, 2.14, and 2.16).

Because concentrations of Al^{3+} in soil water remain high throughout the year (see Chapter 7), one must conclude that the trees in the MMor and Mor forest plots are most probably subject to chronic rather than short-term Al-toxicity. *Neitske* [1984] reported that prolonged exposure (>20 weeks) of beech roots to soil solutions with Ca^{2+}/Al^{3+} $\leq$1.0 leads to a similar degree of root damage as that observed during short-term exposure to Ca^{2+}/Al^{3+} values <0.1. Similarly, reduced root elongation was observed for spruce when exposed to solutions of Ca^{2+}/Al^{3+} <1.0 or Ca^{2+}/H^+ <0.5 [*Tischner et al.*, 1983; *Rost-Siebert*, 1985]. Injuries to the root system (rhizo-toxicity) primarily concern the tips of the roots which leads, in turn, to reduced nutrient uptake [*Roy et al.*, 1988] and to the development of shallow root systems, thus increasing the plant's sensitivity to drought and restricting its ability to explore the soil for nutrients [*Foy et al.*, 1978; *Marschner*, 1991]. Other effects of excess Al on ecosystem functioning relate to the complexation of P [*Roy et al.*, 1988], retarded litter decomposition because of adversely affected micro-flora [*Moloney et al.*, 1983], a tendency towards selective transport of carbohydrates and amino acids to the roots rather than to the above-ground parts [*Simon and Rothe*, 1985], and the enhanced release of root exudates (including phenolic compounds) [*Whipps and Lynch*, 1986]. The synthesis of the latter may consume >30 % of the total plant production in some cases [*Whipps and Lynch*, 1986].

Trees growing in high acidity, high Al^{3+} environments show various tolerance mechanisms, including deposition of Al in cell walls and vacuoles where it cannot damage metabolism [*Cuenca et al.*, 1990]. High concentrations of Al (>1000 $\mu g\, g^{-1}$) in leaves of stunted montane tropical trees have been reported for Sri Lanka [*Werner*, 1988] and various sites in Venezuela [*Steinhardt*, 1979; *Cuenca*

Table 2.15: Chemical composition of litter percolate and soil water extracted from various tropical soils. All values ($\mu mol\, l^{-1}$) represent ceramic cup lysimeter extractions (at -30 to -60 *kPa*) except for the data of *Jordan* [1989] (free-drainage) and *Steinhardt* [1979] (actual tension). Data by *Nortcliff and Thornes* [1989] represent averages of wet and dry season concentrations.

Locality	Soil type	Depth [cm]	Ca	Mg	K	Na	Al	NH_4	NO_3	N_{tot}	PO_4	P_{tot}
			[all in $\mu mol\, l^{-1}$]									
Lowland forests:												
Brasil[1]	Ferralsol	15 to 120	4.6	12.8	26.9	87.8	-	-	-	-	-	-
Guyana[2]	Ferralic arenosol	120	29.7	18.9	23.5	230.9	6.7	18.3	106.4	-	-	-
North Costa Rica[3]	Dystric cambisol	70	13.3	28.8	8.6	68.6	-	2.5	107.4	-	0.16	-
East Malaysia[4]	litter percolate		18.9	24.8	86.3	-	-	31.4	121.3	-	1.19	-
	Orthic acrisol	30 to 50	12.2	19.1	22.6	-	-	2.9	111.4	-	0.23	-
Montane forests:												
East Malaysia[5] (680 *m*)	litter percolate		114.7	104.8	132.3	228.3	3.3	53.9	251.8	373.3	0.8	<2.0
	Humic cambisol	7	96.0	<225.5	188.5	548.0	13.0	27.0	120.0	-	2.3	-
		18	10.0	49.0	71.0	381.5	8.0	49.5	267.5	-	2.5	-
		45	23.0	121.5	20.5	185.0	<2.5	8.0	161.0	-	<0.3	-
(870 *m*)	litter percolate		132.0	98.8	84.0	142.0	<5.3	58.5	167.0	350.2	0.8	<2.0
	Dystric cambisol	15	123.3	23.0	21.3	124.0	4.7	36.3	283.3	-	<0.3	-
		45	141.7	41.3	22.3	135.7	<2.7	19.0	268.3	-	1.1	-
Venezuela[6]	Humic cambisol	humus	126.7	86.1	18.0	212.7	39.2	-	-	325.7	-	9.39
		20	20.0	22.7	35.3	24.2	61.3	-	-	57.1	-	1.03
		90	10.3	4.7	11.5	11.7	6.7	-	-	55.0	-	0.52
Jamaica[7]; WMull	litter percolate		106.5	68.8	142.7	84.1	8.8	74.2	177.7	183.6	0.33	3.25
	Dystric cambisol	Ah, 0–14	38.7	54.5	45.5	61.3	18.9	11.3	94.8	67.1	0.45	0.67
	Dystric cambisol	B, 30–89	16.2	22.8	12.3	63.9	1.8	5.0	31.4	41.1	0.34	0.45
Jamaica[7]; Mor	litter percolate		137.1	96.2	89.4	106.1	2.4	23.7	2.2	151.3	0.18	2.04
	Folic histosol	Ah, 0–9	14.4	39.4	16.5	50.6	58.4	8.2	4.4	59.0	0.26	0.99
	Folic histosol	Bw, 19–54	7.0	13.8	5.0	43.4	2.6	8.4	18.4	51.5	0.31	1.17

[1] *Nortcliff and Thornes* [1989]; [2] *Brouwer* [1996]; [3] *Parker* [1985]; [4] *Burghouts* [1993]; [5] *Bruijnzeel et al.* [1993], *Waterloo* [1989]; [6] *Steinhardt* [1979]; [7] this study.

Table 2.16: Molar concentrations of 'free' ions of aluminium, hydrogen and base cations and their ratios based on thermodynamic speciation calculations (PHREEQC; *Parkhurst* [1995], *Driscoll and Schecher* [1988]) of selected soil moisture samples from the Ah-horizons of the study plots ($n = 3$).

Forest	Al^{3+}	H^+	Ca^{2+}	K^+	Mg^{2+}	Na^+
			[all in $\mu mol\, l^{-1}$]			
WMull	1.14	11.22	37.02	40.19	53.69	60.89
PMull	1.46	15.74	6.17	7.20	15.81	56.59
MMor	14.52	81.37	9.19	9.00	28.88	57.88
Mor	19.48	132.50	14.15	16.49	38.60	50.58

Forest	$\frac{Ca^{2+}}{Al^{3+}}$	$\frac{K^+}{Al^{3+}}$	$\frac{Mg^{2+}}{Al^{3+}}$	$\frac{Na^+}{Al^{3+}}$	$\frac{Al^{3+}}{H^+}$	$\frac{Ca^{2+}}{H^+}$	$\frac{K^+}{H^+}$	$\frac{Mg^{2+}}{H^+}$	$\frac{Na^+}{H^+}$
WMull	32.47	35.25	47.10	53.41	0.10	3.30	3.58	4.79	5.43
PMull	4.22	4.92	10.81	38.71	0.09	0.39	0.46	1.00	3.60
MMor	0.63	0.62	1.99	3.99	0.18	0.11	0.11	0.35	0.71
Mor	0.73	0.85	1.98	2.60	0.15	0.11	0.12	0.29	0.38

et al., 1990] but *Gautam-Basak and Proctor* [1983] found much lower foliar Al in the leaves of a stunted montane forest compared with those of a larger-statured forest on Gunung Mulu, Sarawak. Concentrations of Al in mature sun leaves of eight principal species in the study forests never reached 1000 $\mu g\, g^{-1}$ although this value occurred occasionally in leaf litter of *Clethra occidentalis* (see Chapter 3 for details on leaf and small root chemistry).

Alternatively, a preference for NO_3^- ions in the presence of NH_4^+ results in an increase of rhizosphere pH, causing removal of Al^{3+} from the soil solution by precipitation and chelation (*Taylor and Foy* [1985]; *cf.* the contrast in NO_3^- and NH_4^+ concentrations between the PMull and MMor sites; Table 2.14). However, although such mechanisms partly ameliorate the toxic effects of Al^{3+}, they probably impose a high ecological cost in terms of photosynthate allocation and growth [*Kuiters*, 1990; *Cuenca et al.*, 1990]. Finally, organic acids and phenolic substances are also known to form strong complexes with Al^{3+}, thereby reducing its toxicity [*Bartlett and Riego*, 1972; *Hue et al.*, 1986]. *Bruijnzeel et al.* [1993] reported concentrations of polyphenols in fresh leaf litter to be about 2.5 times higher in stunted montane forest than in taller-statured forest on the same mountain in East Malaysia. A similar contrast in concentrations was found in the soil moisture extracted from the Ah-horizons of the Mor and Mull forests (Table 2.12) which also exhibits large differences in concentrations of Al^{3+} (*c.* 15–20 $\mu mol\, l^{-1}$ *vs. c.* 1–1.5 $\mu mol\, l^{-1}$, respectively; Table 2.12).

Polyphenols have been shown to interfere negatively with litter decomposition and various metabolic processes such as photosynthetic rates, cell division in fine roots, stomatal aperture and ion uptake (see review by *Kuiters* [1990]). On the other hand, *Jordan et al.* [1979] showed that nitrification rates in Amazonian forest growing on an acid Ferralsol were suppressed. They hypothesized that the low nitrification rates were the result of high tannin concentrations in the root mat and interpreted their findings as a strategy of the forest to

limit nitrogen losses by reducing the production of highly mobile NO_3^-. More recently, *Northup et al.* [1995] demonstrated the occurrence of an inverse relationship between soil pH and foliar concentrations of phenols which coincided with reduced concentrations of NO_3^- and increased concentrations of dissolved organic N (DON) in soil moisture under increasingly acid concentrations (*cf.* Table 2.12). They interpreted these trends as a mechanism whereby the forests conserve mobile NO_3^- via complexation with organic compounds such as phenols. They further hypothesized that the trees would somehow be able to reaccess the temporarily bound N at a later stage, *e.g.* with the help of specific mycorrhizae. Further work is necessary to demonstrate whether similar processes are at work in stunted montane tropical forests, such as the (M)Mor forests of the study area. Some support for the hypothesis of *Northup et al.* [1995] comes from the fact that concentrations of NO_3^- in the Mor-type topsoils were much lower than in the Mull-type topsoils whereas the opposite was true for DON (Table 2.12). Although the net overall effect of enhanced polyphenols in the Mor-type ecosystem may therefore well be positive, it is likely that the production of these secondary metabolites comes at a high cost [*Kuiters*, 1990] and thus, as in the case of enhanced root exudates and rhizosphere alkalinization [*Taylor and Foy*, 1985; *Whipps and Lynch*, 1986], may be at the expense of above-ground biomass production.

2.5 Conclusions

The present data on the structure and floristics of the PMull and MMor forests basically justified their classification as intermediate forest types within the Mor–WMull sequence recognized by *Tanner* [1977a, 1980b]. Besides main canopy height, the density of multiple-stemmed trees and the trunk/tree ratio (but not plot basal area and tree density) proved to be indicative of the relative ranking of the forests. The trend in species diversity (decreasing from Mull to Mor) were somewhat obscured by contrasts in plot size and enumeration limits between the present study and those by Tanner. No significant differences were found between (specific) leaf area and (specific) leaf mass of principal tree species in the PMull and MMor forests but three out of four species showed significant thicker leaves in the MMor forest.

Differences in soil development in Mull- and Mor-type forests were striking: Mull profiles are characterized by relatively thin ectorganic horizons whereas Mor profiles have a 30–50 *cm* thick layer of slowly decomposing humus and a root mat. Acidity and degree of Al-saturation in the Mor soils are both much higher than in the Mull-type soils, possibly due to high concentrations of organic acids leached from the accumulating humus. Both the biodiversity and abundance of soil fauna, including fungi, litter fragmenters and predators, were higher in litter from the PMull forest compared to the MMor.

Physical soil characteristics in both the PMull and MMor forests prevent prolonged soil saturation. Persistent waterlogging can therefore not be held responsible for the contrasts in forest physiognomy observed in the study area.

Although the waterholding capacity of the more shallow (M)Mor forest soils, and the distribution of small roots therein, may indicate an enhanced sensitivity to drought compared to the deeper PMull soils, the local rainfall regime (>3000 $mm\,yr^{-1}$) makes the frequent occurrence of such long dry spells highly unlikely. As such, the contrasts in stature among the forest plots do not seem to reflect substantial differences in soil water dynamics (see also Sections 5.5.4 and 5.6.4).

Previous studies on foliar analysis [*Tanner*, 1977b] in the study area indicated gradually decreasing concentrations of key elements (N, P, K, Ca) in foliage and leaf litterfall from tall- to short-statured forest as well as a significant increase in trunk growth after (heavy) additions of N and P to the forest soil [*Tanner et al.*, 1990], suggesting that one (or all) of these elements may limit forest growth. However, the present findings do not support a straightforward relationship between forest stature and soil nutrient status as the concentrations of ammonium-acetate extractable nutrients in the respective forest soils do not parallel the forest sequence based on stature. Furthermore, although concentrations of most key nutrient elements (including NO_3^-,NH_4^+, PO_4^{3-} and K^+) in litter percolate parallel the ranking of the four forests on the basis of stature (as do concentrations of NO_3^- and NH_4^+ in soil water extracted from the Ah-horizons), concentrations of base cations, total N and PO_4^{3-} in topsoil water do not show such a pattern. In addition, concentrations of key elements, except for mineral N, in soil water extracted from the Ah-horizon are found to be high in the most 'impoverished' (Mor) forest whereas the elemental concentrations in both litter percolate and soil moisture are not consistently below those reported for montane localities elsewhere, including those that carry tall (>30 m) montane forest Table 2.15.

Summarizing, it seems plausible that not intrinsically low nutrient availability is *the* important factor determining the physiognomy of the montane forests in Jamaica but that the nutrient uptake capacity of the stunted forests is somehow restricted, be it by high concentrations of H^+ (in case of K) or by high concentrations of phenolic compounds in soil moisture (in case of N).

Both concentrations of phenols, H^+ and, consequently, Al^{3+} in top soil water in the Mor-type forests greatly exceed concentrations in the Mull-type forests. Concentrations of Al^{3+} in Mor-type soil water exceed values that are thought to indicate Al-toxicity [*Cronan and Grigal*, 1995]. As the effect is believed to be chronic rather than temporary, limitations to the nutrient uptake capacity of the roots in the Mor-type forests are expected. Furthermore, high concentrations of Al^{3+} in soil moisture may initiate the formation of strong Al–P complexes, thereby reducing P-availability to plants, retard litter decomposition and enhance the below-ground exudation of secondary metabolites, including polyphenols, to reduce its toxicity. The present findings provide some support for the hypothesis of *Northup et al.* [1995] that phenols may also reduce the formation of mobile NO_3^- in favour of dissolved organic nitrogen, and also conserve NO_3^- via complexation and prevent excessive losses of mobile N via leaching. Concentrations of NO_3^- were indeed much lower in Mor- than in Mull-type topsoil water whereas the opposite was found for both DON and phenols. Although the net effect of enhanced phenol concentration in the Mor-type for-

est may therefore be positive, it is likely that the enhanced production of these secondary metabolites comes at a high ecological cost in terms of photosynthate allocation, the result of which may be a retardation in forest growth.

3

PRELIMINARY OBSERVATIONS ON FOLIAR AND SMALL ROOT CHEMISTRY IN FOUR MONTANE FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA

ABSTRACT

The degree of accumulation of aluminium and polyphenols in leaves, litter and small roots was investigated in relation to the chemistry of litter percolate and soil water in a sequence of four montane forests of contrasting stature and soil acidity in the Blue Mountains of Jamaica. Concentrations in foliage at various stages of age and in fresh litter from seven principal tree species and in bulk root samples from the four forests were analyzed for N, P, base cations, aluminium and phenols.

Despite the fact that acidity and Al^{3+} in topsoil water of the stunted Mor-type forests were much higher than in the Mull-type forests, Al concentrations in mature leaves of the latter (0.07–0.19 $mg\,g^{-1}$) were higher than in Mor forests (0.05 and 0.13 $mg\,g^{-1}$). The contrasts between sites were small for young leaves, increased with leaf age and were largest for leaf litterfall (c. 0.11 $mg\,g^{-1}$ in the Mor forests vs. 0.13–0.45 in the Mull forests). None of the investigated tree species classified as a true Al-accumulator.

Concentrations of K and P were very low in leaves from all forests and of all age classes and species (<2.5 and <1.6 $mg\,g^{-1}$, respectively) and may indicate K and P deficiency. Surprisingly, P was lowest in leaves from from the tallest forest (<0.5 $mg\,g^{-1}$). Concentrations of Ca and Mg, and to a lesser extent Al, increased with leaf age whereas concentrations of K and P decreased. Contrasts between phenol concentrations in leaf fall of different ages and from different forest types were very small. Foliar concentrations of K, and to a lesser extent Al, paralleled forest stature, but Mg showed an inverse trend. Concentrations of K, Al, and total N in small roots decreased with decreasing forest stature. No significant inter-site differences were observed for Ca, Mg, P and phenols in small roots between short-statured Mor- and tall Mull-type forest. No evidence was found for an inverse relationship between soil pH and polyphenols in mature leaves or small roots, neither between phenol and Al concentrations or N concentrations.

The relatively high Al concentrations in small roots, litter and old leaves in the tall

WMull forest may reflect an Al-accumulating strategy that includes Al translocation of complexed (non-toxic) Al to cell walls and vacuoles. Based on the observed contrasts in Al in old leaves and litter between Mor- and Mull-type forests it seems plausible that Mor trees are unable to do this. Instead the Mor forest trees may detoxify Al^{3+} *by below-ground exudation of chelating compounds (including phenols) to form non-toxic organic-Al complexes. This strategy probably comes at a high ecological cost and may reduce above-ground forest growth.*

3.1 INTRODUCTION

In a recent review of tropical montane forest productivity, *Bruijnzeel and Veneklaas* [1998] acknowledged the scarcity of information on the overall carbon economy of tropical montane forests and the influence of climate and soil conditions thereupon. In addition, they emphasized that comparisons of site conditions and ecological processes in forests of contrasting stature on single mountains are usually hampered by: (i) differences in climatic conditions at different elevations; (ii) changes in soil type with elevation, and (iii) differences in species composition [*Proctor et al.*, 1988, 1989; *Grieve et al.*, 1990; *Veneklaas and Van Ek*, 1990; *Bruijnzeel et al.*, 1993; *Pendry and Proctor*, 1996a, b; *Liebermann et al.*, 1996]. There is merit, therefore, in focussing on the differences in edaphic conditions experienced by forests of contrasting stature but with similar species assemblages under (nearly) similar climatic conditions [*Hetsch and Hoheisel*, 1976; *Tanner*, 1977a].

A striking example of the latter situation is found in the Blue Mountains of Jamaica where between 1500 and 1850 *m* a.s.l. a series of forests is found with increasingly acid humus and topsoil (pH 4.4–3.0) and a gradual reduction in forest stature from so-called 'Well-developed' Mull forest (WMull, canopy height 13–17 *m*) via intermediate 'Poorly-developed' Mull forest (PMull, 7–12 *m*) and 'Moderately-developed' Mor forest (MMor, 5–8 *m*) to stunted Mor forest (Mor, 5–7 *m*) [*Tanner*, 1977a, 1980b, *cf.* Chapter 2]. In the early years of the century *Shreve* [1914] ascribed the contrasts in forest stature in the study area largely to differences in atmospheric humidity (read: contrasting exposure to fog and low cloud). Later, *Tanner* [1977a, 1985] and *Healey* [1990] emphasized contrasts in soil fertility. *Bruijnzeel* [1989a] drew attention to the fact that the annual inputs of nutrients to Jamaica's montane forests via bulk precipitation [*Tanner*, 1977a] greatly exceeded the amounts incorporated annually as trunk biomass [*Tanner*, 1985], suggesting that either the nutrients become immobilized upon entering the soil or that either the uptake capacity of the roots is limited by some factor. *Bruijnzeel et al.* [1993] hypothesized that high concentrations of polyphenols in leaves and soil moisture could be such a factor. Concentrations of phenols are known to be influenced by a wide range of biotic and abiotic stress factors [*Gershenzon*, 1984]. They themselves, however, can also affect a wide range of ecological processes, including ion uptake [*Kuiters*, 1990]. Phenolic concentrations in litter percolate and topsoil moisture in stunted Mor-type

forest in Jamaica were found to be about four times higher than in Mull-type forest (Table 2.12 in Chapter 2) although concentrations in Mor leaf litter were only moderately (and not significantly) higher. Also, aluminium concentrations in soil moisture extracted from the topsoil of the Mor-type forests were 2–3 times higher than in the PMull (Table 2.12). In addition, concentrations of Al^{3+} in Mor-type soil water exceeded values that are thought to indicate Al-toxicity [*Cronan and Grigal*, 1995]. In short, the roots of the Mor forests trees seem to be exposed to more adverse edaphic conditions than those in the Mull, including higher acidity, higher Al^{3+} and phenolic concentrations, which are believed to be detrimental to root functioning, either alone or in combination [*Foy et al.*, 1978; *Simon and Rothe*, 1985; *Whipps and Lynch*, 1986; *Roy et al.*, 1988; *Marschner*, 1991; *Cronan and Grigal*, 1995]. Consequently, the aim of this chapter is to investigate the degree of accumulation (or absence) of aluminium and polyphenols in foliage and small roots in relation to the corresponding concentrations in litter percolate and soil water in the cited sequence of four montane forests of contrasting stature in the Blue Mountains of Jamaica.

3.2 Study sites

A detailed description of the structure and floristic composition of the PMull and MMor forests has been given in Chapter 2 whereas *Tanner* [1977a, 1980b] provides comparative information for the Mor and (W)Mull forests. Details on soil, litter, and water chemistry for the four forests have been summarized in Chapter 2.

Forest composition
The species composition of the four forests is similar (Section 2.3.1) but the relative contribution of principal tree species varies between forest types. Also, total tree species diversity is higher in the Mull-type forests (Table 3.1). Principal species include *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, *Clethra occidentalis*, *Chaetocarpus globosus*, *Alchornea latifolia* and *Podocarpus urbanii*; Mor forest is characterized by large numbers of *L. octandra* and the terrestrial epiphyte *Clusia* cf. *havetioides* as well as by a higher occurrence of *Vaccinium meridionale*. On the other hand, of the more typical Mull forest species *C. occidentalis*, *P. urbanii* and *Hedyosmum arborenscens* [*Tanner*, 1977a, 1980a, b], only *Clethra occidentalis* occurs in significant numbers in the MMor forest as well (Table 3.1). The dominant leaf size is microphyllous–notophyllous whereas the leaves are often hard and leathery and considered scleromorphous [*Tanner and Kapos*, 1982].

Edaphic conditions, solid phase
In the two Mull forests a discontinuous litter/fermentation layer (<4 *cm*) plus a thin layer of mull humus (*c.* 2 *cm*) overlie deep clay soils (fresh bedrock at >3 *m*) classified as Dystric cambisols. The shallow (≤ 0.7 *m*) Mor forest soils (Folic histosols) have a thick layer of accumulated mor humus (≤ 50 *cm*) and a

Table 3.1: The seven investigated principal tree species, their abbreviations (Abbr.) as used in the tables and diagrams in this chapter and their percentage contribution to total plot basal area. Included are trees with d.b.h. $\geq$5 *cm* (MMor and PMull plots) or with d.b.h. $\geq$3.2 *cm* (Mor and Mull plots; *Tanner* [1977a]).

Principal species	Abbr.	(W)Mull	PMull	MMor	Mor
		Contribution to basal area (%)			
Alchornea latifolia	Alc.	5.5	15.1	0.7	9.9
Chaetocarpus globosus	Cha.	4.8	16.0	8.9	17.0
Clethra occidentalis	Cle.	21.7	6.3	5.7	3.8
Clusia cf. *havetioides*	Clu.	0.1	1.6	3.3	9.3
Cyrilla racemiflora	Cyr.	21.9	20.0	23.4	13.7
Lyonia cf. *octandra*	Lyo.	4.9	12.7	45.5	36.8
Vaccinium meridionale	Vac.	2.3	1.8	6.6	2.8
others		38.8	26.5	5.9	6.7
Number of tree species		34	23	10*	16

*believed to be underestimated by 40 % due to a smaller plot size (see Section 2.4.1, for details).

well-developed surface root mat. The pH_{CaCl_2} of litter in the Mull forests sites is 4.6–5.0, compared to 4.3–4.5 for Mor material (Table 2.10). Acidity increases with depth, with minimum values in the lower part of the ectorganic layers. Top soil acidity ranges from pH 4.2 to pH 3.4 and the pH-based ranking parallels that for forest stature: (W)Mull>PMull>MMor$\gtrsim$Mor.

Although by and large mull-type litter has higher $BaCl_2$-extractable concentrations of, especially, Mg and K (but not Ca), and of oxalate-extractable P, no clear trend emerges for Al^{3+} or Al-saturation of litter material (Table 2.10). However, concentrations of $BaCl_2$-extractable Al^{3+} tend to be higher in the F+H layers and the Ah-horizons of the Mor-type forests than in the Mull-type forests. The same holds for NH_4^+ and oxalate-extractable P in topsoil material.

Edaphic conditions, liquid phase

The pH of litter percolate (*LP*) and topsoil water follow the trends observed for the pH_{H_2O} of the soils (Tables 2.10 and 2.12). Minimum values occur in the Ah-horizons. Clear declining trends are observed for the concentrations of most nutrients in litter percolate and topsoil moisture in the WMull to the MMor forest sequence, whereas concentrations of total Al in topsoil moisture increase steadily throughout the sequence as well. However, for some unknown reason, concentrations of nutrients in *LP* and Ah moisture in the Mor forest exceed those for both the similarly-statured MMor and the taller PMull (Section 2.3.3). More importantly, however, whilst concentrations of total Al in soil water in the Mor forest are 2–3 times higher than those in the Mull forests, the contrast becomes even more pronounced for Al^{3+}, viz. 15–20 *vs.* 1–1.5 $\mu mol\, l^{-1}$, respectively (Fig. 2.9). The increases in concentrations of total Al from the WMull to the Mor forest are parallelled by increases in the concentrations of polyphenols and dissolved organic carbon (DOC) (Table 2.12).

3.3 MATERIAL AND METHODS

Field sampling
Live canopy leaves (both young and old) were collected in April 1997 for seven principal tree species in each of the four forest sites. The sampled species included: Euphorbiaceae: *Alchornea latifolia*, *Chaetocarpus globosus*; Clethraceae: *Clethra occidentalis*; Guttiferae: *Clusia* cf. *havetioides*; Cyrillaceae: *Cyrilla racemiflora*; and Ericaceae: *Lyonia* cf. *octandra*, *Vaccinium meridionale* (*cf.* Table 3.1). Approximately forty young and forty old, sunlit leaves without signs of herbivory were taken from each of five trees per species per forest. Young leaves were assumed to be those leaves that were still small and had a lighter green colour compared to mature leaves. Old leaves were assumed to be those leaves that were fully grown and heavily discoloured.

Earlier, a set of mature (*i.e.* not old, but larger and darker coloured than the presently sampled young leaves) sunlit leaves had been collected in December 1994 from the same dominant species plus *Podocarpus urbanii* (Podocarpaceae) in each of the four forest types. Twenty to forty mature leaves without signs of herbivory or discolouring were taken from the upper canopy of 4–6 trees per species per site and bulked per tree. No distinction between leaves of different age were made at the time. The surface areas of the leaves were determined by weighing pieces of paper of the same size as the leaves to the nearest 0.001 g and converting these to surface areas via a predetermined conversion factor. Values of specific leaf area (SLA) were obtained by dividing surface area by the corresponding dry weight (measured to the nearest 0.001 g after drying to constant weight at 50 $^{\circ}C$). No SLA value was determined for the leaves of *Podocarpus urbanii*. Because the WMull and Mor plots of *Tanner* [1977a, 1980b] are used for long-term observations of forest dynamics, care was taken to sample in the vicinity of the plots rather than in the plots themselves.

Freshly fallen litter without signs of decomposition was picked up randomly for each species from the surface of the litter layer. Samples of live foliage were bagged separately per tree, whereas litter was bulked per species per plot. Collections were oven-dried at 50 $^{\circ}C$ for 24 hours, ground (1–4 mm) and stored until transportation to Amsterdam. A relatively low temperature was maintained for the drying to prevent evaporation of phenolic compounds [*Kuiters*, 1990]. Small-root samples were taken from each forest from the transition layer between the H- and Ah-horizons, *i.e.* from the section of the soil having the highest density of small (<2 mm) roots [*Elbers*, 1996]. Only bulk samples of about 50 g (taken from a 10×10 cm segment; $n = 13$ per site) were collected because roots from different species could not be distinguished. The roots were rinsed in water to remove any adhering soil- and litter particles, rinsed again with demineralised water and dried at 50 $^{\circ}C$ for 24 h. All roots were <3 mm in diameter.

Analytical procedures
Leaves, litter and small roots were redried in Amsterdam (50 $^{\circ}C$, 24 h) and ground in a centrifugal ball mill to pass through a 0.10-mm sieve. Of the 280

foliar samples (5 individuals×7 species×4 forests×2 age classes), samples for the 5 individual trees per species, forest and leaf age were bulked into a single sample as part of a preliminary analysis*. Of the mature leaves collected in 1994 all samples ($n = 158$) were analyzed; of the 13 small-root samples per site 7 were analyzed for cations (Ca, Mg, K, and Al), P and polyphenols whereas all 13 were analyzed for C and N.

Samples of approximately 0.15 *g* were digested in $HNO_3/HClO_4$ at 150 *℃* and 1.5 *MPa* pressure for 25 minutes using a micro-wave/pressure bomb method [*Smit*, 1995]. Digestions were analyzed for P, Ca, K, Mg, and Al by ICP-AES emission (Perkin-Elmer 6500). The quality of digestions and analyses were controlled using one sample of reference material (olive leaves, genus *Olea europaea*; BCR-CRM 062, no. 0535) and one blank sample per 10 samples analyzed. Nitrogen and carbon were determined using a Carlo Erba 1600 elemental analyser. Phenolic compounds were analyzed using the method described by *Box* [1983] and *Waterman and Mole* [1994]. Samples of 0.10 *g* (with one blanc per 16 samples) were extracted for 1 *h* in 8.0 *ml* aqueous methanol (50 % by volume) and frequently shaken. The methanol extracts were centrifuged (5 *min.* at 3000 *rpm*) for the sedimentation of solids. Total phenol concentrations were measured photometrically using Folin-Ciocalteau reagents (Merck, art nr. 1.09001.0100). Absorbance was measured at 760 *nm* relative to a solution series of pure tannic acid powder (Merck, art. nr. 1.00773.0250). Concentrations of phenolic compounds were expressed as tannic acid equivalents (TAE).

3.4 Results

3.4.1 Foliar chemistry

Although not statistically demonstrable at this stage because of the lack of analytical replication, trends in nutrient concentrations of leaves sampled in April 1997 at different stages of leaf development apparently differ for many of the species investigated. Values for the respective elements per species, leaf type (young leaves, old leaves, fresh leaf litter) and forests are given in Tables 3.2 and 3.3 but the contrasts are more readily recognized from Fig. 3.1 (Ca, Mg, K) and Fig. 3.2 (P, Al, polyphenols). No adequate amount of old leaves of sufficient quality could be collected for *Clethra occidentalis* in the Mor-type forests and for *Vaccinium meridionale* in the Mor and WMull forests. The values in Tables 3.2 and 3.3 therefore refer to the 1994 data for mature leaves (Table 3.6).

For a given species, concentrations of Ca and, to a lesser extent, phenols remain reasonably constant for different leaf ages and forest types although there are a few exceptions (*e.g. C. occidentalis*, Fig. 3.1). For all species, except perhaps for *V. meridionale*, concentrations of Mg tend to decrease with increasing forest stature (*i.e.* from Mor to WMull); concentrations of K often, but not always, reduce with leaf age (as seems also to be the case for P) and by and large increase from short-statured Mor-type forest to the taller Mull-type

*Analysis of the complete sample set is planned for the year 2000.

forests. The reduction of K concentrations with leaf age is particularly strong for *Clethra*, *Clusia* and *Cyrilla*, less well pronounced for *Alcornea*, *Chaetocarpus* and *Lyonia*, and basically absent for *Vaccinium* (Table 3.1). Concentrations of P (Fig. 3.2) are high in young foliar material from the Mor plots (where they are also reduced with leaf age) but are remarkably low in all Mull foliar material, including young leaves (Fig. 3.2). For many elements, the trends with leaf age appear to be especially pronounced for *C. occidentalis* (*e.g.* K), even when such trends seem absent for other species, for example in the case of Ca (increasing with age) or phenolic compounds (decreasing with age; Fig. 3.2). As for Al concentrations, no consistent trends for leaf age or forest type are obvious, except perhaps for *Lyonia* cf. *octandra* (increasing with leaf age and higher in Mull- compared to Mor forests). Contrasts between leaf types and/or sites are large for different species (Fig. 3.2). *Foy et al.* [1978] proposed a foliar Al concentration of 1000 $\mu g\, g^{-1}$ as a lower limit for true aluminium accumulator plants. Applying this criterion to the present data shows that none of the investigated tree species classifies as a true Al-accumulator. Only litter of *C. occidentalis* in the WMull forest had an Al concentration in excess of 1000 $\mu g\, g^{-1}$ (1014 $\mu g\, g^{-1}$) but the concentrations in young and old foliage for this species did not exceed 190 and 230 $\mu g\, g^{-1}$, respectively. Fresh litter of *Lyonia* cf. *octandra* also had relatively high concentrations of Al (400 $\mu g\, g^{-1}$; Table 3.3).

Weighted average element concentrations per plot based on the basal area contributions of the seven principal species give a clear picture of the differences between the four forest types (Table 3.4, Fig. 3.3). Better results might have been obtained by weighting the contributions of individual species to annual leaf litterfall but these are unknown for the WMull and Mor forests. The two methods gave comparable results for the PMull and MMor forests because a significant correlation ($r^2 > 0.59$, $P < 0.05$) was found between basal area and litter contribution for these two forests (see Section 8.4.1).

Although the trend is probably absent in the WMull forest, increases in Ca concentrations with leaf age appear to be stronger for the shorter-statured Mor plots compared to the Mull-type forests. Concentrations of Mg are stable with leaf age but tend to be reduced in young leaves with increasing forest stature. An inverse pattern is observed for K, *i.e.* concentrations increase steadily from the Mor to the WMull forest (Fig. 3.3). Concentrations of both K and P decreased rapidly with leaf age. Especially striking are the very low concentrations of P in all leaf types in the tallest forest of all, the WMull. Concentrations of Al generally increase with leaf age. The contrasts are especially marked for WMull foliage/litter but are only modest or non-existent (old leaves *vs.* litter in the MMor forest) in the other forests. A slight increase in foliar Al concentrations with forest stature may be observed but the trend is not convincing. No clear patterns emerge for concentrations of phenolic compounds (Fig. 3.3).

3.4.2 Chemical composition of small roots

Concentrations of K and Al, and to a lesser extent N and P in small roots parallel the forest ranking based on tree stature as concentrations increase towards the

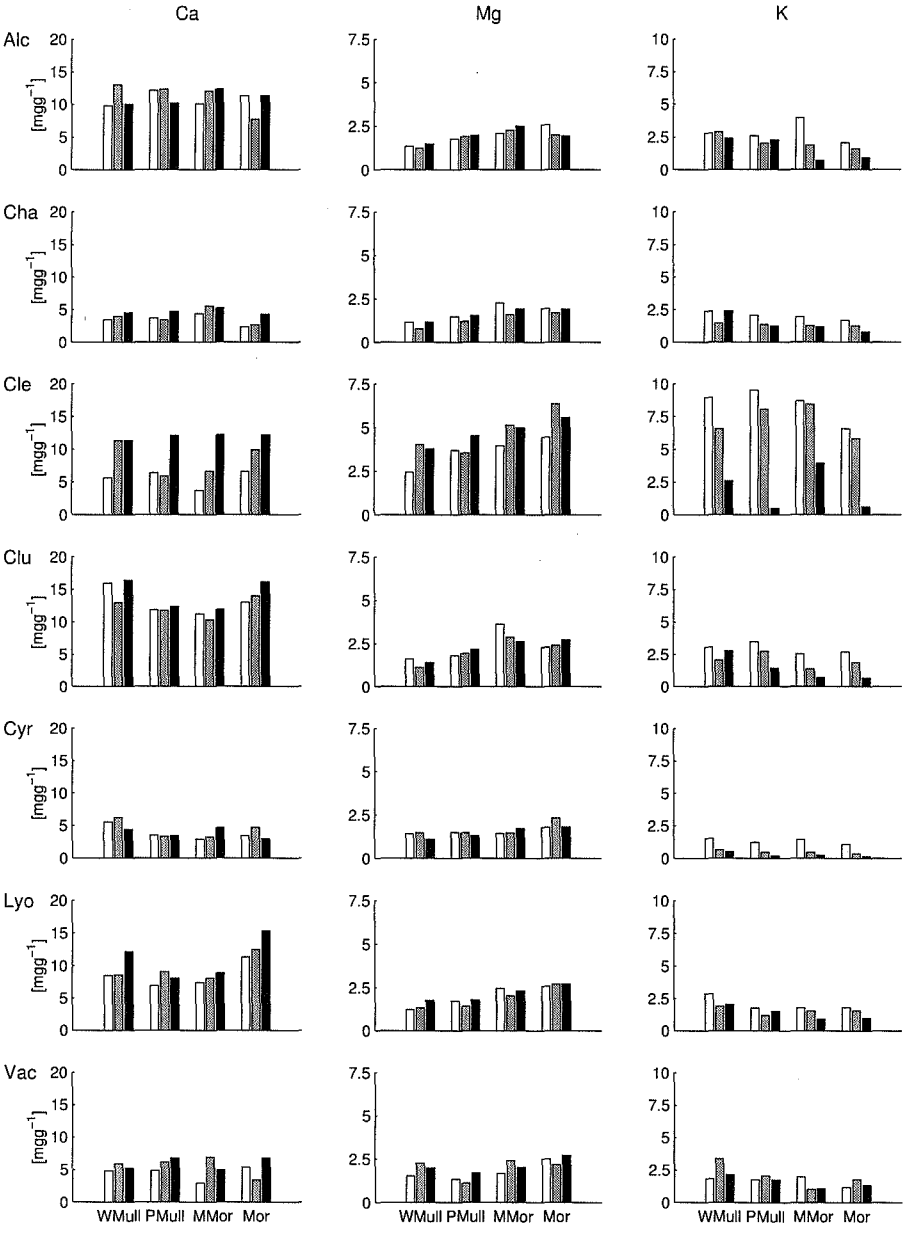

Figure 3.1: Concentrations ($mg\,g^{-1}$) of Ca, Mg, and K in young leaves (white bars), old leaves (grey bars), and fresh leaf litter (black bars) for seven principal tree species in, successively, the WMull, PMull, MMor, and Mor forests.

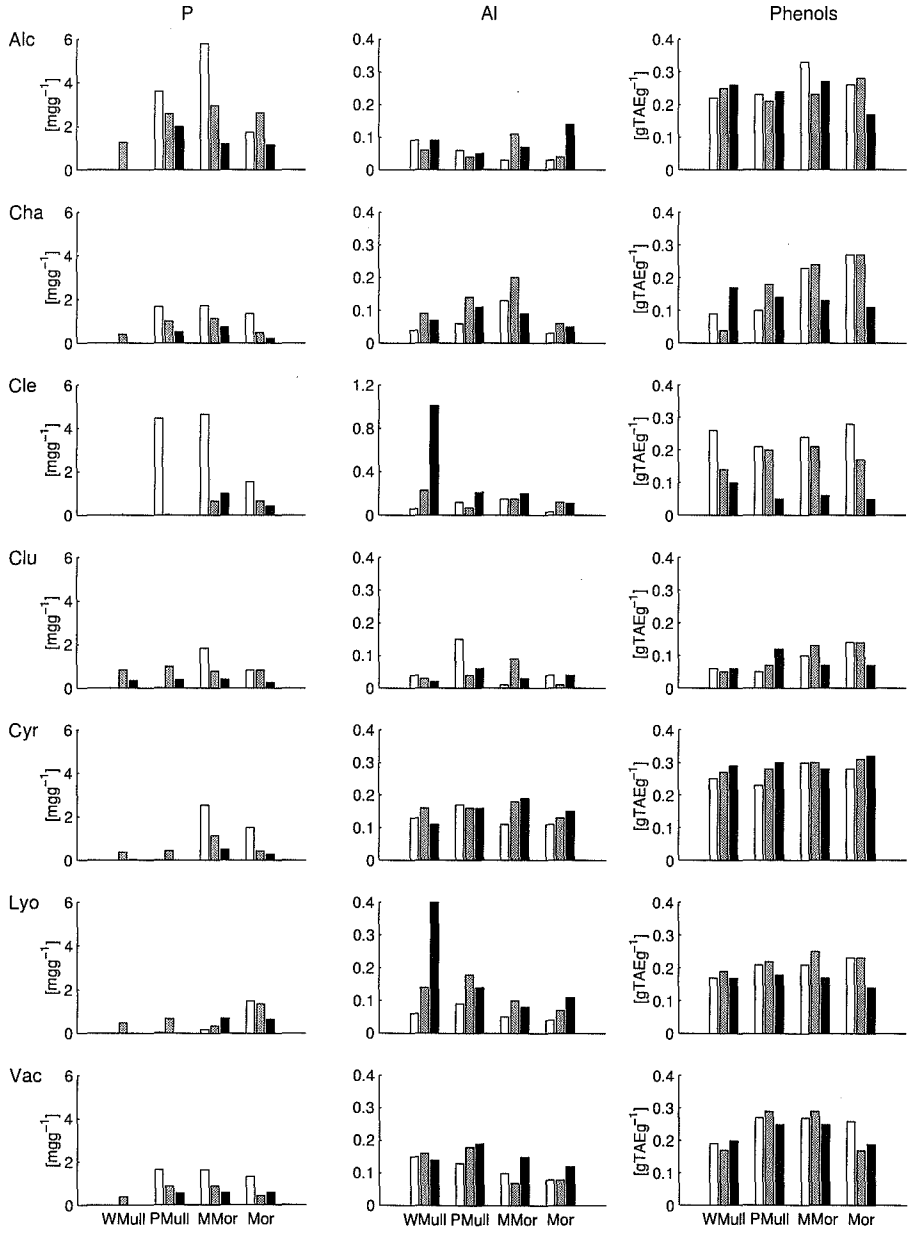

Figure 3.2: Concentrations of Al and P ($mg\,g^{-1}$) and phenolic compounds ($g\,\mathrm{TAE}\,g^{-1}$) in young leaves (white bars), old leaves (grey bars), and fresh leaf litter (black bars) for seven principal tree species in, successively, the WMull, PMull, MMor, and Mor forests.

Table 3.2: Concentrations of Ca, Mg, and K ($mg\,g^{-1}$) in young leaves (y.l.), old leaves (o.l.) and fresh leaf litter (l.l.) collected in April 1997 for seven principal tree species in four forest types. Species abbreviations as in Table 3.1.

Species	Forest	Ca [$mg\,g^{-1}$]			Mg[$mg\,g^{-1}$]			K [$mg\,g^{-1}$]		
		y.l.	o.l.	l.l.	y.l.	o.l.	l.l.	y.l.	o.l.	l.l.
Alc.	WMull	9.79	13.02	10.04	1.36	1.23	1.47	2.79	2.89	2.39
	PMull	12.13	12.33	10.18	1.78	1.91	1.97	2.60	2.01	2.27
	MMor	10.07	12.05	12.32	2.09	2.27	2.51	3.94	1.84	0.69
	Mor	11.30	7.70	11.30	2.58	2.00	1.93	2.05	1.58	0.93
Cha.	WMull	3.42	4.00	4.55	1.14	0.78	1.17	2.35	1.44	2.39
	PMull	3.68	3.44	4.73	1.47	1.19	1.53	2.05	1.35	1.22
	MMor	4.37	5.57	5.23	2.26	1.61	1.91	1.95	1.26	1.15
	Mor	2.34	2.68	4.26	1.94	1.70	1.90	1.66	1.26	0.79
Cle.	WMull	5.64	11.30	11.31	2.43	4.03	3.78	8.96	6.57	2.60
	PMull	6.39	5.92	12.13	3.69	3.55	4.52	9.53	8.06	0.50
	MMor	3.73	6.67†	12.19	3.96	5.15†	4.99	8.67	8.43†	3.91
	Mor	6.62	9.89†	12.21	4.44	6.34†	5.57	6.58	5.81†	0.61
Clu.	WMull	15.99	13.00	16.42	1.61	1.11	1.41	3.04	2.03	2.77
	PMull	11.93	11.81	12.39	1.81	1.94	2.15	3.47	2.74	1.43
	MMor	11.28	10.34	11.95	3.64	2.88	2.61	2.53	1.36	0.68
	Mor	13.03	14.00	16.17	2.29	2.40	2.71	2.68	1.86	0.67
Cyr.	WMull	5.55	6.22	4.41	1.40	1.48	1.11	1.53	0.63	0.51
	PMull	3.49	3.36	3.44	1.49	1.47	1.31	1.22	0.47	0.20
	MMor	2.89	3.25	4.65	1.43	1.48	1.71	1.46	0.43	0.25
	Mor	3.47	4.72	2.98	1.79	2.32	1.81	1.08	0.37	0.14
Lyo.	WMull	8.50	8.58	12.15	1.24	1.31	1.76	2.87	1.89	2.03
	PMull	6.90	9.08	8.07	1.71	1.41	1.79	1.77	1.20	1.53
	MMor	7.38	8.09	8.88	2.46	2.04	2.31	1.76	1.55	0.90
	Mor	11.35	12.46	15.33	2.58	2.70	2.70	1.79	1.56	0.98
Vac.	WMull	4.84	5.90†	5.20	1.54	2.27†	2.00	1.81	3.36†	2.15
	PMull	4.88	6.15	6.79	1.33	1.12	1.71	1.75	2.07	1.75
	MMor	2.92	6.94	4.99	1.66	2.42	2.04	1.96	1.03	1.07
	Mor	5.37	3.38†	6.76	2.51	2.18†	2.71	1.17	1.76†	1.34

†no data for old leaves available; values refer to the 1994 data for mature leaves (Table 3.6).

tall-statured WMull forest (Table 3.5, Fig. 3.4). Concentrations of all elements are highest in the latter forest type except for total carbon (higher in Mor-type forests) and phenolic compounds (highest in PMull). Concentrations differed significantly between the shortest-statured (Mor) and the tallest forest (WMull) for K, Al, and N. No significant contrasts were observed for Ca, Mg, and P whereas phenolic compounds only differed significantly between the PMull and WMull forests but not between Mull and Mor-type forests (Table 3.5, Fig. 3.4).

3.5 Discussion

3.5.1 Foliar and root chemistry

Mature leaves vs. *young/old leaves*: The more or less steady decrease in the concentrations of Ca, K, Al and N in mature leaves from *A. latifolia*, *C. occidentalis* and, to a lesser extent, *V. meridionale* with decreasing forest stature agrees with the observations of *Tanner* [1977a] for foliar concentrations of N and K of *A. latifolia* and *C. occidentalis* sampled in March 1974 in a series of forest

Table 3.3: Concentrations of P, Al ($mg\,g^{-1}$) and phenolic content ($g\,\mathrm{TAE}\,g^{-1}$) in young leaves (y.l.), old leaves (o.l.) and fresh leaf litter (l.l) collected in April 1997 for seven principal tree species in the four forest types. Species abbreviations as in Table 3.1.

Species	Forest	P [$mg\,g^{-1}$]			Al [$mg\,g^{-1}$]			Phenols [$g\,\mathrm{TAE}\,g^{-1}$]		
		y. l.	o. l.	l. l.	y. l.	o. l.	l. l.	y. l.	o. l.	l. l.
Alc.	WMull	-	1.26†	-	0.09	0.06	0.09	0.22	0.25	0.26
	PMull	3.59	2.58	1.99	0.06	0.04	0.05	0.23	0.21	0.24
	MMor	5.78	2.96	1.18	0.03	0.11	0.07	0.33	0.23†	0.27
	Mor	1.73	2.63	1.16	0.03	0.04	0.14	0.26	0.28	0.17
Cha.	WMull	0.01	0.41†	0.00	0.04	0.09	0.07	0.09	0.04	0.17
	PMull	1.66	1.02	0.53	0.06	0.14	0.11	0.10	0.18	0.14
	MMor	1.72	1.14	0.74	0.13	0.20	0.09	0.23	0.24	0.13
	Mor	1.36	0.50	0.23	0.03	0.06	0.05	0.27	0.27	0.11
Cle.	WMull	0.02	0.01	0.00	0.06	0.23	1.01	0.26	0.14	0.10
	PMull	4.46	0.02	0.00	0.12	0.07	0.21	0.21	0.20	0.05
	MMor	4.65	0.65†	0.99	0.15	0.15†	0.20	0.24	0.21†	0.06
	Mor	1.54	0.66†	0.43	0.03	0.12†	0.11	0.28	0.17†	0.05
Clu.	WMull	0.01	0.84	0.35	0.04	0.03	0.02	0.06	0.05	0.06
	PMull	0.02	0.99	0.39	0.15	0.04	0.06	0.05	0.07	0.12
	MMor	1.83	0.78	0.40	0.01	0.09	0.03	0.10	0.13	0.07
	Mor	0.82	0.82	0.27	0.04	0.01	0.04	0.14	0.14	0.07
Cyr.	WMull	0.00	0.37†	0.03	0.13	0.16	0.11	0.25	0.27	0.29
	PMull	0.00	0.43†	0.00	0.17	0.16	0.16	0.23	0.28	0.30
	MMor	2.53	1.13	0.49	0.11	0.18	0.19	0.30	0.30	0.28
	Mor	1.51	0.43	0.28	0.11	0.13	0.15	0.28	0.31	0.32
Lyo.	WMull	0.00	0.47†	0.00	0.06	0.14	0.40	0.17	0.19	0.17
	PMull	0.05	0.66†	0.02	0.09	0.18	0.14	0.21	0.22	0.18
	MMor	0.17	0.33	0.69	0.05	0.10	0.08	0.21	0.25	0.17
	Mor	1.48	1.36	0.65	0.04	0.07	0.11	0.23	0.23	0.14
Vac.	WMull	0.00	0.39†	0.00	0.15	0.16†	0.14	0.19	0.17†	0.20
	PMull	1.64	0.89	0.57	0.13	0.18	0.19	0.27	0.29	0.25
	MMor	1.64	0.89	0.57	0.10	0.07†	0.15	0.27	0.29	0.25
	Mor	1.31	0.43†	0.58	0.08	0.08†	0.12	0.26	0.17†	0.19

not available; †no data available for old leaves; values refer to the 1994 data for mature leaves (Table 3.6).

types not unlike the present sequence. However, the increase in foliar concentrations of P in the two species with increasing stature reported by *Tanner* [1977a] is only partly supported by the present data set (increases for *A. latifolia* and *Podocarpus urbanii*; decreases for *C. occidentalis* and *V. meridionale*; Table 3.6). Such contrasting findings illustrate the difficulties associated with the interpretation of foliar analyses [*cf. Tanner*, 1977a]. Nevertheless, species whose foliar concentrations in mature leaves roughly follow the ranking of the forests based on stature (notably *A. latifolia*, *C. occidentalis* and *V. meridionale*) often also rank high when sorting species on the basis of average nutrient concentrations (Table 3.10). Conversely, species that show relatively small contrasts between forests (*C. racemiflora* and *C. globosus*) often rank low (Table 3.10). Similar trends emerge when species are sorted for their nutrient concentrations in young and old leaves, especially for base cations, P, and Al (*cf.* Tables 3.2 and 3.3). A large contrast, however, is noted for *C. racemiflora* which is positioned at the low end of the sequence for Al and phenols in mature leaves (Table 3.6)

Table 3.4: Weighted average concentrations of nutrients ($mg\,g^{-1}$) in young, old, and freshly fallen leaves in the four forest types (see text for explanation of weighting procedure).

Forest	Leaf type	Ca	Mg	K	P	Al	Phenols
				$[mg\,g^{-1}]$			$[g\,\mathrm{TAE}\,g^{-1}]$
WMull	young	6.02	1.73	4.46	0.01	0.09	0.23
	old	8.65	2.32	3.21	0.34	0.17	0.19
	litter	8.04	2.18	1.75	0.03	0.45	0.20
PMull	young	6.36	1.77	2.55	1.53	0.10	0.19
	old	6.68	1.70	1.84	1.03	0.12	0.22
	litter	6.93	1.88	1.17	0.55	0.13	0.21
MMor	young	5.60	2.26	2.18	1.38	0.08	0.24
	old	6.59	2.11	1.62	0.70	0.13	0.28
	litter	7.54	2.29	0.95	0.65	0.12	0.19
Mor	young	8.34	2.39	1.95	1.42	0.05	0.24
	old	8.81	2.49	1.54	1.09	0.07	0.24
	litter	10.77	2.46	0.78	0.52	0.10	0.16

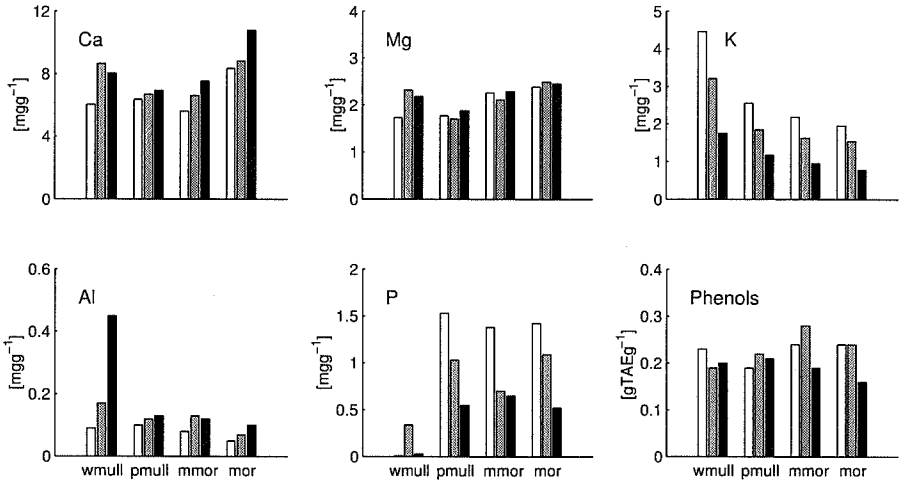

Figure 3.3: Weighted average concentrations of nutrients in young (white bars), old (grey bars) and freshly fallen leaves (black bars) in the four forest types (see text for explanation of weighting procedure).

Table 3.5: Mean elemental concentrations ($mg\,g^{-1}$) and phenolic concentrations ($mg\,\mathrm{TAE}\,g^{-1}$) of bulk samples of small roots ($n = 7$) in the WMull, PMull, MMor, and Mor forests.

Forests	Ca	Mg	K	Al	P	N	C†	Phenols
				$[mg\,g^{-1}]$			$[g\,g^{-1}]$	$[mg\,\mathrm{TAE}\,g^{-1}]$
WMull	7.81	2.04	1.66_{abc}	5.81_{a}	0.03	14.49_{abc}	0.48	16_{a}
PMull	5.69	1.74	1.05_{ad}	5.33_{b}	0.01	10.70_{ad}	0.47	47_{a}
MMor	5.53	1.55	0.89_{b}	2.06	0.01	6.69_{bde}	0.51	23
Mor	7.65	1.92	0.54_{cd}	0.37_{ab}	0.01	7.10_{ce}	0.49	38

Values in one column followed by the same letter are significantly different ($P < 0.05$); †all values for total carbon (C) are significantly different between forests at $P < 0.05$.

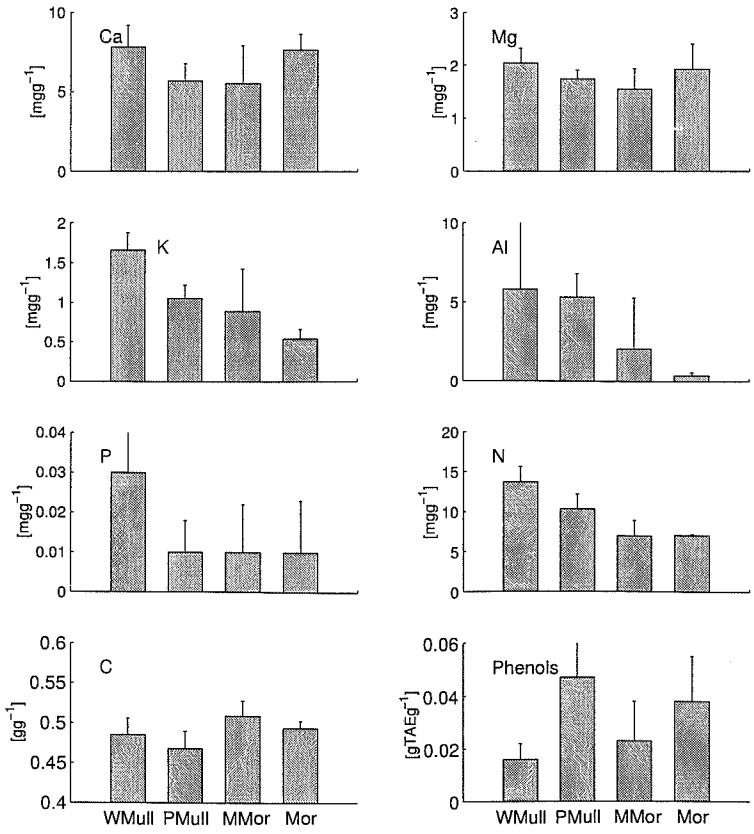

Figure 3.4: Mean elemental concentrations ($mg\,g^{-1}$) and phenolic concentrations ($g\,\mathrm{TAE}\,g^{-1}$) in bulk samples of small roots ($n = 13$ for C and N; $n = 7$ for others) in, successively, the WMull, PMull, MMor, and Mor forests.

and at the top end for both young and old leaves. It is possible that seasonal variations in concentrations are part of the explanation but little to nothing is known about such variations in the study area (or indeed anywhere else).

Tanner et al. [1998] emphasized the need to express nutrient concentrations on the basis of leaf area rather than leaf mass because leaf area is more closely related to the primary function of leaves (which is to absorb light). *Vitousek et al.* [1992] and *Medina et al.* [1981] reported foliar concentrations of key elements (including P and N) to be similar or to decrease with elevation when expressed on a mass basis but to increased on an area basis due due to the corresponding decrease in SLA . Table 3.7 expresses the nutrient concentrations in mature leaves on the basis of leaf area by dividing the values given in Table 3.6 by the corresponding specific leaf areas (see Section 2.2.1 for details). SLA values for a specific species were not significantly different between the PMull, MMor, and Mor forests but were indeed higher for the WMull forest (*cf.* Table 2.1). The resulting contrasts in weight and area based concentrations between the respective forest types, however, are small (compare Tables 3.6 and 3.7).

The generally decreasing concentrations of K with leaf age (Fig. 3.1) can be explained by the fact that K is usually retranslocated from old leaves to younger foliar tissue in order to minimize element losses, especially on nutrient-poor soils [*Vitousek*, 1984]. The strikingly low concentrations of K in leaves of all classes and species (mostly <2.5 $mg\,g^{-1}$, except for *C. occidentalis*, Tables 3.2 and 3.6) were also found by *Tanner* [1977a]. The presently found concentrations are far below the range for healthy broad-leaved tropical trees (typically 5–30 $mg\,g^{-1}$) and fall within the range that may indicate deficiency symptoms (1.0–3.0 $mg\,g^{-1}$) [*Drechsel and Zech*, 1991]. The clear decrease in weighted average K concentrations in both young leaves, old leaves and fresh litter when going from tall-statured to short-statured forest (Fig. 3.3) is more or less paralleled by the patterns observed for K in litter percolate (Table 2.12). Such findings underline the importance of nutrient retention mechanisms like retranslocation before leaf abscission. Theoretically, K deficiency in the soil may be intensified by high concentrations of Al because Al^{3+} has been shown to be an effective blocker of cation channels in root cell plasmatic membranes and this inhibits the uptake of K^+ [*Kochian*, 1995; *Lüttge*, 1997]. However, the similarity in the trends found for overall K and Al concentrations in both leaves (Fig. 3.3) and small roots (Fig. 3.4) in the Mor—WMull forest sequence suggests no such adverse influence of Al, despite the much higher concentrations in topsoil moisture in the Mor-type forests (Table 2.12). It therefore remains to be seen if these forests do indeed experience a true K deficiency and, if so, whether this is caused or intensified by excessive Al in the soil.

A more direct way of assessing the presence or degree of K (or any other) deficiency is a comparison of inputs and outputs of K (or other nutrients) to and from the forest floor via net precipitation and litterfall decomposition, and uptake and drainage, respectively. Nutrient budgets for the respective elements in the PMull and MMor forests will be presented in Chapters 7 (nutrient fluxes in water), 8 (litter dynamics) and 9 (decomposition).

Table 3.6: Average elemental concentrations on a dry weight basis ($mg\,g^{-1}$; carbon in $g\,g^{-1}$; phenols in $g\,\mathrm{TAE}\,g^{-1}$) in mature, sunlit foliage as collected in the four forest types in December 1994. Values are arithmetic means of 5 samples per species per forest type.

Species	Forest	Ca	K	Mg	Al	P	N	C	Phenols
Alc.	WMull	10.04	7.04	2.31	0.12	1.26	15.68	0.45	0.089
	PMull	7.44	5.36	1.72	0.09	1.12	13.86	0.47	0.227
	MMor	8.42	4.58	2.67	0.10	1.19	13.72	0.47	0.212
	Mor	5.62	5.25	1.84	0.05	0.99	12.97	0.46	0.141
Che.	WMull	4.46	6.13	1.62	0.09	0.41	9.09	0.48	0.133
	PMull	2.20	4.81	1.25	0.04	0.55	8.13	0.50	0.161
	MMor	5.11	2.65	1.94	0.13	0.42	7.66	0.50	0.176
	Mor	3.52	3.05	1.57	0.07	0.46	4.88	0.50	0.178
Cle.	WMull	6.93	16.03	3.46	0.19	0.57	10.54	0.44	0.023
	PMull	7.65	10.90	4.95	0.19	0.62	10.16	0.46	0.197
	MMor	6.67	8.43	5.15	0.15	0.65	9.73	0.46	0.214
	Mor	9.89	5.81	6.34	0.12	0.66	9.25	0.46	0.172
Clu.	WMull	15.70	8.09	1.49	0.07	0.49	7.70	0.48	0.129
	PMull	10.07	5.28	1.99	0.07	0.45	6.31	0.48	0.093
	MMor	10.22	5.12	2.59	0.05	0.43	5.85	0.48	0.100
	Mor	13.81	3.28	2.52	0.07	0.51	7.57	0.48	0.131
Cyr.	WMull	2.95	3.55	1.11	0.08	0.37	8.15	0.50	0.131
	PMull	1.83	2.97	1.05	0.08	0.43	5.29	0.50	0.157
	MMor	1.95	3.07	0.95	0.10	0.49	5.31	0.50	0.137
	Mor	1.74	1.92	1.01	0.05	0.40	10.25	0.51	0.110
Lyo.	WMull	8.83	4.36	1.33	0.14	0.47	8.67	0.51	0.171
	PMull	9.06	3.94	1.47	0.12	0.66	8.64	0.51	0.160
	MMor	6.52	4.55	2.11	0.10	0.60	8.71	0.51	0.181
	Mor	9.34	3.64	1.73	0.13	0.53	9.17	0.51	0.159
Pod.	WMull	8.76	8.29	2.03	0.09	0.48	8.19	0.46	0.015
	PMull	6.12	3.25	1.31	0.13	0.53	7.52	0.48	0.111
	MMor	9.53	3.98	1.48	0.12	0.54	6.95	0.47	0.121
	Mor	12.07	4.28	1.54	0.10	0.55	6.59	0.47	0.033
Vac.	WMull	5.90	3.76	2.27	0.16	0.39	7.73	0.50	0.171
	PMull	4.21	3.33	1.83	0.12	0.41	8.68	0.50	0.160
	MMor	2.24	3.72	1.52	0.07	0.45	7.90	0.50	0.205
	Mor	3.38	1.76	2.18	0.08	0.43	7.92	0.51	0.167

Table 3.7: Average elemental concentrations on a leaf area basis* ($\mu g\, cm^{-2}$; carbon in $mg\, cm^{-2}$; phenols in $mg\,\mathrm{TAE}\, cm^{-2}$) in mature, sunlit foliage as collected in the four forest types in December 1994. Values are arithmetic means of 5 samples per species per forest type.

Species	Forest	Ca	K	Mg	Al	P	N	C	Phenols
Alc.	WMull	121.4	85.2	28.0	1.5	15.2	189.6	5.5	1.1
	PMull	128.7	92.6	29.7	1.5	19.4	239.5	8.1	3.9
	MMor	141.1	76.7	44.7	1.7	19.9	230.0	7.8	3.6
	Mor	82.3	76.9	26.9	0.8	14.4	190.0	6.7	2.1
Cha.	WMull	57.5	79.0	20.9	1.2	5.3	117.2	6.2	1.7
	PMull	39.2	85.8	22.3	0.7	9.8	145.0	8.9	2.9
	MMor	102.8	53.3	38.9	2.6	8.4	153.9	10.1	3.5
	Mor	70.6	61.1	31.6	1.3	9.2	97.9	10.0	3.6
Cle.	WMull	73.8	170.7	36.8	2.1	6.0	112.2	4.7	0.2
	PMull	110.9	158.0	71.8	2.7	8.9	147.2	6.7	2.9
	MMor	90.0	113.9	69.6	2.0	8.8	131.4	6.2	2.9
	Mor	156.3	91.8	100.3	1.8	10.5	146.3	7.3	2.7
Clu.	WMull	524.1	270.0	49.8	2.2	16.4	257.2	16.0	4.3
	PMull	298.5	156.6	58.9	1.9	13.2	187.2	14.2	2.7
	MMor	310.0	155.3	78.5	1.5	13.0	177.3	14.7	3.0
	Mor	436.0	103.6	79.7	2.1	16.0	239.2	15.1	4.1
Cyr.	WMull	42.9	51.7	16.2	1.2	5.4	118.4	7.3	1.9
	PMull	31.8	51.5	18.2	1.3	7.5	91.7	8.7	2.7
	MMor	31.5	49.7	15.4	1.5	8.0	85.9	8.2	2.2
	Mor	28.1	31.2	16.4	0.9	6.5	166.2	8.2	1.8
Lyo.	WMull	168.3	83.1	25.3	2.7	9.0	165.2	9.6	3.3
	PMull	157.2	68.3	25.5	2.0	11.4	149.9	8.8	2.8
	MMor	108.1	75.5	35.0	1.7	9.9	144.4	8.5	3.0
	Mor	138.2	53.8	25.6	2.0	7.8	135.7	7.5	2.4
Vac.	WMull	102.6	65.4	39.4	2.8	6.8	134.5	8.7	3.0
	PMull	64.7	51.2	28.2	1.9	6.3	133.3	7.7	2.5
	MMor	35.0	58.2	23.8	1.1	7.1	123.7	7.9	3.2
	Mor	51.5	26.9	33.2	1.2	6.5	120.6	7.7	2.5

*values in Table 3.6 divided by the corresponding specific leaf area (SLA); SLA values are arithmetic averages of 4–6 samples (identical to those for chemical analysis) per species per site; see Chapter 2 for details.

Table 3.8: Weighted average concentrations of nutrients ($mg\, g^{-1}$; carbon in $g\, g^{-1}$; phenol concentrations in $g\,\mathrm{TAE}\, g^{-1}$) in mature, sunlit leaves as collected in December 1994 in the four forest types (see text for explanation of weighting procedure).

Forest	Ca	K	Mg	Al	P	N	C	Phenols
				$[mg\, g^{-1}]$				$g\,\mathrm{TAE}\, g^{-1}$
WMull	6.31	8.52	2.21	0.12	0.52	9.46	0.47	0.08
PMull	5.15	4.62	1.64	0.09	0.64	8.65	0.49	0.17
MMor	5.10	4.20	1.97	0.10	0.55	7.71	0.50	0.17
Mor	7.10	3.45	1.88	0.09	0.55	8.74	0.50	0.15

Table 3.9: Overview of species with increasing or decreasing nutrient concentrations in mature foliage in the sequence from short-statured Mor forest to tall-statured WMull forest. *Clethra occidentalis* and *Alchornea latifolia* (grey boxes) have been accentuated to emphasize their frequent occurrence. Abbreviations as in Table 3.1.

	Increasing	Decreasing
Ca	Alc , Vac	Cle , Pod
K	Cle , Vac, Cha, Clu, Cyr	-
Mg	-	Cle , Clu
Al	Alc , Cle , Vac	-
P	-	Cle , Vac, Pod
N	Alc , Cle , Cha, Pod	Lyo

Table 3.10: Ranking of eight principal tree species on the basis of the chemical composition of mature foliage as collected in December 1994. *Clethra occidentalis*, *Alchornea latifolia* (grey boxes), *Chaetocarpus globosus* and *Cyrilla racemiflora* (white boxes) have been marked to emphasize their relative positions. Abbreviations as in Table 3.1.

Element	Ranking
Ca	Clu $\gg$ Pod $>$ Lyo $\simeq$ Alc $=$ Cle $\gg$ Vac $\simeq$ Cha $>$ Cyr
Mg	Cle $\gg$ Alc $\simeq$ Clu $\gtrsim$ Pod $>$ Lyo $=$ Cha $>$ Vac $\gtrsim$ Cyr
K	Cle $\gg$ Alc $=$ Clu $>$ Vac $>$ Lyo $\simeq$ Cha $=$ Pod $>$ Cyr
Al	Cle $>$ Lyo $\gtrsim$ Vac $=$ Pod $>$ Alc $>$ Cha $\simeq$ Cyr $>$ Clu
P	Alc $\gg$ Cle $\gtrsim$ Lyo $\gtrsim$ Pod $\gtrsim$ Clu $\gtrsim$ Cha $\simeq$ Vac $=$ Cyr
N	Alc $\gg$ Cle $>$ Lyo $\gtrsim$ Vac $\gtrsim$ Cha $\simeq$ Pod $=$ Cyr $>$ Clu
Phenols	Vac $\gtrsim$ Alc $=$ Lyo $\gtrsim$ Cha $>$ Cle $>$ Cyr $>$ Clu $\gg$ Pod
C	Lyo $\gtrsim$ Cyr $=$ Vac $\gtrsim$ Cha $>$ Clu $>$ Pod $>$ Alc $\gtrsim$ Cle

In addition to the seemingly deficient levels of K in the foliage and litter of the Jamaican forests, concentrations of P also fall below the optimum range suggested by *Drechsel and Zech* [1991] (<1.0 $mg\,g^{-1}$), especially in the WMull forest. Although the currently found trends for concentrations of P in mature leaves from the respective forests sometimes parallel those reported by *Tanner* [1977a] for individual species (*e.g.* an increase from Mor to WMull for *A. latifolia* (Table 3.6), the nearly doubled average concentration of P in the leaves of Tanners's [1977b] tallest forest (Gap forest, comparable to WMull) compared to that in the Mor forest (1.0 *vs.* 0.5 $mg\,g^{-1}$) is not confirmed by the present data (Tables 3.3 and 3.6). The reasons for this discrepancy are unclear but it cannot be caused by the fact that the early estimates represent arithmetic averages and the present ones weighted averages (Table 3.4).

Small roots: The low concentrations of P in WMull foliage are perhaps related

to the relatively high concentrations of Al in the leaves of this forest (Fig. 3.3, Tables 3.4 and 3.6). Aluminium has been shown to be able to precipitate phosphate in the apoplasts of roots in the form of poorly soluble $Al_2(PO_4)_3$ and this reduces P availability to the leaves [*Lüttge*, 1997]. Some support for this contention comes from the finding that both Al and P in small roots are increased in the WMull (Fig. 3.4). With the exception of P, which shows a more or less inverse pattern to that observed in the foliage of the respective forests, element concentrations in small roots reflect the corresponding trends in foliar chemistry. Concentrations of N, K, and Al increase towards the taller-statured forests whereas those of Ca and Mg are comparable for the four forest types (Fig. 3.4). There are few comparative data on (small) root chemistry in tropical montane forests but compared to tall LMRF in Venezuela, Papua New Guinea and Puerto Rico the roots in the present forests are low in P and K (and to a lesser extent Mg but not in Ca) as well as N in the Mor-type forests (Table 3.11). Compared to the only published estimate for Al concentrations in fine roots in any tropical montane rain forest [*Steinhardt*, 1979], concentrations in the present Mull-type forests seem elevated and those in Mor-type forests low (Table 3.11). Also, concentrations of Al in small roots are much higher than those in foliage, both in the Jamaican forests (Tables 3.4 and 3.5) and in the Venezuelan forest (3.4 *vs.* 1.8 $mg\,g^{-1}$; *Steinhardt* [1979]). Whilst Al concentrations in the leaves of some upper montane rain forests in Sri Lanka and Venezuela have been shown to be very high (up to 11 $mg\,g^{-1}$; *Werner* [1988]; *Cuenca et al.* [1990]), the presently found foliar concentrations are modest (Tables 3.4 and 3.6). Also, *Gautam-Basak and Proctor* [1983] found much lower Al concentrations in the leaves of a stunted UMRF in Sarawak than in a taller forest lower down the same mountain, possibly because of differences in underlying rock types (Al-deficient sandstones *vs.* Al-containing shales). The role of Al in the study forests is discussed further below.

3.5.2 Aluminium toxicity

In an extensive review of the effects of soil aluminium levels on plant growth, *Cronan and Grigal* [1995] considered the molar ratio Ca^{2+}/Al^{3+} a useful indicator of aluminium-induced stress. They suggested a 50 % risk of adversely affected tree growth when Ca^{2+}/Al^{3+} in soil solutions fell below 1.0 whereas chances would rise to 90 % for $Ca^{2+}/Al^{3+} \leq 0.1$. The Ca^{2+}/Al^{3+} values in Table 3.12 demonstrate that there is a risk of Al-induced stress in the Mor-type forests. Ca^{2+}/Al^{3+} ratios in water extracted from the Mor-type Ah-horizons are typically smaller than 0.75 whereas values in the Mull-type Ah-horizons range between 4 and 33 (*cf.* Table 2.12). As will be demonstrated later (Chapter 7), concentrations of Al in soil water in the Mor-type forests remain high throughout the year, implying that the trees are subject to chronic rather than to short-term Al-toxicity. *Neitske* [1984] reported that prolonged exposure (>20 weeks) of beech (*Fagus sylcatica*) roots to soil solutions with $Ca^{2+}/Al^{3+} \geq 1.0$ leads to a similar degree of root damage as that observed during short-term exposure to Ca^{2+}/Al^{3+} values <0.1 [*cf. Tischner et al.*, 1983; *Rost-Siebert*, 1985].

Table 3.11: Nutrient concentrations ($mg\,g^{-1}$) in (small) roots (diameter class added where available) fin selected wet tropical forests.

Location	Forest type	Root type	Ca	Mg	K	Al	P	N
			[all in $mg\,g^{-1}$]					
San Carlos, Venezuela[1]	Tierra Firme	fine	2.1	2.6	6.7	-	1.13	23.0
	tall Caatinga	fine	3.0	3.9	8.3	-	0.95	10.4
	low Bana	fine	3.5	3.7	12.2	-	0.51	8.4
New Guinea[2]	tall LMRF	<5 *mm*	7.3	6.1	4.1	-	0.33	7.4
El Verde, Puerto Rico[3]	LMRF	<5 *mm*	1.4–19.4	0.3–0.8	0.7–1.4	-	0.15–0.61	2.9–13.2
San Eusebio, Venezuela[4]	LMRF	<5 *mm*	4.9	1.3	2.4	3.4	0.49	8.2
Jamaica								
WMull[5]	UMRF	<3 *mm*	7.8	2.0	1.7	5.8	0.03	14.5
PMull[5]	UMRF	<3 *mm*	5.7	1.7	1.1	5.3	0.01	10.7
MMor[5]	UMRF	<3 *mm*	5.5	1.6	0.9	2.1	0.01	6.7
Mor[5]	UMRF	<3 *mm*	7.7	1.9	0.5	0.4	0.01	7.1
Mor[6]	UMRF	<2 *cm*	11.4	1.2	1.0	-	0.1	2.5

[1] *Cuevas and Medina* [1988]; [2] *Edwards and Grubb* [1982]; [3] *Ovington and Olson* [1970], minimum and maximum values for 36 tree species; [4] *Steinhardt* [1979]; [5] present study; [6] *Tanner* [1985].

Cronan and Grigal [1995] also suggested that molar Ca/Al ratios in fine root tissue of 0.2 or smaller and in foliar tissue of 12.5 or smaller could serve as supplementary indices of Al-induced stress (both indicative of a 50 % risk). Except for leaf litter in the WMull, these limits were not exceeded for the root and foliar material in the study forests (Table 3.12). Although topsoil moisture shows increasing Ca^{2+}/Al^{3+} ratios towards tall-statured WMull forest, values for small roots and foliage show an opposite trend (Table 3.12). Despite being exposed to similar Ca^{2+}/Al^{3+}in the soil solution, the corresponding ratios found in root and leaf material in the Mor forest are, respectively, nearly 8 and 2–3 times those found for the MMor, suggesting that another factor may be at work.

3.5.3 The role of phenolic compounds

The relatively high Al concentrations of small roots, litter and old leaves in the tall WMull forest may be caused by an Al-accumulating strategy that does not necessarily reflect high Al tolerance but is more likely the result of root-induced chelation of Al in the rhizosphere and translocation of complexed (non-toxic) Al to the leaves [*Cuenca et al.*, 1990; *Marschner*, 1991]. It may be hypothesized on the basis of the relative contrasts in Al in old leaves and freshly fallen litter between Mor- and Mull-type forests (Table 3.4) that the trees in the Mor-type forests do not (or are unable to) return excess Al to the forest floor via litterfall

Table 3.12: Molar ratios of Ca/Al in small roots, foliar material (young, old, mature and freshly fallen leaves) and in moisture extracted from the Ah-soil horizons. Ratios in tissues are based on total element concentrations; ratios in soil moisture refer to speciated Ca^{2+} and Al^{3+}.

Forest	Soil moisture*	Small roots†	Foliar material			
			young°	old°	mature*	litter°
WMull	33	0.9	45	34	53	12
PMull	4.0	0.7	43	38	57	36
MMor	0.6	2.0	47	34	51	42
Mor	0.7	14	112	85	79	73

*Table 2.12; †Table 3.5; °Table 3.4; *Table 3.8.

by concentrating Al in their leaves prior to abscission to the same degree as the trees in the WMull forest. As will be shown in Chapter 8, although data on Al in leaf litterfall in the WMull and Mor forests are lacking, the amounts of Al in small litterfall in the PMull are roughly 3 to 4 times those in the MMor forest, thus confirming the contrast suggested in Table 3.4. In view of the fact that the roots of the trees in the Mor forest are subjected to more adverse edaphic conditions (lower pH, higher Al^{3+} and lower Ca^{2+}/Al^{3+} ratios) than those in the WMull (*cf.* Tables 2.12 and Table 3.12), the impression arises that the mechanism of translocating chelated Al-compounds to foliar cell walls and vacuoles (where they do not damage cell metabolism; *Cuenca et al.* [1990]) as proposed for the Mull-type forest does not function under the conditions prevailing in the Mor-type forests. Further studies are needed to test this contention. However, the high Ca/Al ratios in root and leaf material in the Mor forest (Table 3.12) suggest that under those conditions another mechanism to reduce Al-toxicity may be at work, viz. Al-exclusion rather than chelation and translocation. Exclusion strategies include alteration of the rhizosphere pH and the release of organic acids and phenolic substances from the root apex [*Kochian*, 1995]. The latter are known to form strong complexes with Al^{3+}, thereby partly ameliorating the toxic effects of this element [*Bartlett and Riego*, 1972; *Hue et al.*, 1986]. However, the synthesis of the released secondary metabolites may consume over 30 % of the total plant production in some cases [*Whipps and Lynch*, 1986] and therefore imposes a high ecological cost in terms of photosynthate allocation and growth rate [*Cuenca et al.*, 1990].

Indirect evidence for the enhanced release of secondary metabolites comes from the concentrations of phenolic compounds in litter percolate and topsoil water which were 2 to 4 times higher in Mor-type forest (Table 2.12). However, it should not be forgotten that concentrations of phenolic compounds in leaves and litter (and, after leaching, also in soil water; *Bruijnzeel et al.* [1993]) are also influenced by a range of stress factors other than high Al [*Kuiters*, 1990]. Under the conditions prevailing in the study area, N-deficiency may be among the most important of these factors (*Horner et al.* [1988]; *cf. Tanner* [1977a]; *cf.* NO_3^- and NH_4^+ in Table 2.12). The effects of high polyphenols in leaves/litter

Table 3.13: Mean concentrations of total phenols and total N in live foliage and leaf litter from various wet tropical mountains (after *Bruijnzeel et al.* [1993]). Values for the Blue Mountains are from Table 3.4; values in brackets refer to weighted mean concentrations in mature live foliage (Table 3.8) and leaf fall collected in 1995 (Table 8.4).

Location	Forest type*	Sample type	N %	Phenols [$mg\,\mathrm{TAE}\,g^{-1}$]
Gunung Silam, Sabah				
680 *m* a.s.l.	tall LMRF	fresh litter	0.82	16
		old litter	1.16	2.9
870 *m* a.s.l.	short LMRF	fresh litter	0.80	41
		old litter	0.98	3.3
Bukit Belalong, Brunei				
200 *m* a.s.l.	LRF	fresh litter	1.04	17
500 *m* a.s.l.	LRF	fresh litter	1.36	10
880 *m* a.s.l.	tall LMRF	fresh litter	1.37	15
Gunung Gedeh, Java				
2000 *m* a.s.l.	tall UMRF	litter	1.45	6
2560 *m* a.s.l.	UMRF	live leaves	1.13	7
		litter	0.48	47
2780 *m* a.s.l.	short UMRF	live leaves	0.87	33
		litter	0.28	36
Blue Mountains, Jamaica				
WMull, 1600 *m* a.s.l.	UMRF	live leaves	[0.95]	190–230 [78]
		fresh litter		200
PMull, 1809 *m* a.s.l.	UMRF	live leaves	[0.87]	190–220 [169]
		fresh litter	[0.77]	210 [80]
MMor, 1824 *m* a.s.l.	UMRF	live leaves	[0.77]	240–280 [171]
		fresh litter	[0.61]	190 [102]
Mor, 1600 *m* a.s.l.	UMRF	live leaves	[0.87]	240 [150]
		fresh litter		150

*LRF: lowland rain forest; LMRF: lower montane rain forest; UMRF: upper montane rain forest.

are complex. On the one hand they have been reported to adversely affect the rate of decomposition and promote mor humus formation [*Coulson et al.*, 1960; *Davies*, 1971], on the other they have been suggested to have a positive effect, *e.g.* by temporarily binding mobile mineral N to prevent its loss via leaching [*Jordan et al.*, 1979; *Northup et al.*, 1995]. *Bruijnzeel et al.* [1993] reported a weak but significant inverse relationship between concentrations of N and phenols in leaves and litter from montane tropical forests. As shown in Table 3.13 and Fig. 3.5, the presently obtained values are not only much higher than those found for various forests in South-east Asia but they also correlate poorly with N concentrations. Such findings suggest that factor(s) other than low N may be responsible for the relatively high concentrations of phenols in the Jamaican forests. Table 3.14 presents rankings of the four forest types according to concentrations of N (both total and mineral forms where applicable), Al and polyphenols in topsoil horizons, soil water, small roots and mature foliage. Although not confirmed by the contents of total N in the topsoil, the availability of mineral-N (approximated by concentrations of NH_4-N and NO_3-N in soil water; Table 2.12) decreases towards the short-statured Mor forest whereas this pattern is also reflected by the N concentrations in both foliage and small roots (Table 3.14). Nitrogen mineralization rates and nitrogen input-output budgets will be examined further in Chapter 9 but basically confirm the presently found trends of lower mineralization and nitrification values in the MMor forest (Table 9.4) and reduced losses of NH_4^+ and NO_3^- via drainage. The latter findings confirm the idea of *Northup et al.* [1995] that phenols may reduce the formation of mobile NO_3^- in favour of dissolved organic nitrogen, and conserve NO_3^- via complexation, preventing excessive losses of mobile N via leaching in the stunted forests.

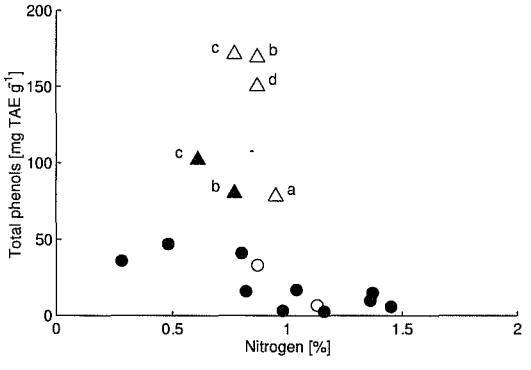

Figure 3.5: Concentrations of total nitrogen (%) and total phenols ($mg\,\mathrm{TAE}\,g^{-1}$) in live leaves (black) and leaf litter (white) from wet tropical mountains (circles, see Table 3.13) and the study forests (triangles; a–d denote the WMull, PMull, MMor, and Mor forests, respectively.

3.6 CONCLUSIONS

The aluminium concentrations and phenolic contents of bulk samples of small roots, foliage and litter (taken from seven principal tree species) from four forest with contrasting stature and soil acidity in the Blue Mountains of Jamaica have been analyzed. The inverse relationship between soil pH and phenolic content of mature leaves, as suggested by *Northup et al.* [1995], was not evident in this study. However, a decrease in concentrations of N in both small roots and foliage towards increasingly stunted forest on gradually more acid soils was parallelled by inverse patterns for concentrations of phenols, Al^{3+} and dissolved organic N (DON) in topsoil water (Table 3.14). Such findings are in line with the idea advanced by *Northup et al.* [1995] that phenols may reduce the formation of mobile NO_3^- in favour of dissolved organic nitrogen, preventing excessive losses of mobile N (NO_3^-) via leaching.

The foliar nutrient status of the four forests did not show the same gradients as one would expect on the basis of differences in their stature. The only plausible trends that emerged from foliar, root, soil, and moisture-chemistry alike, are the unfavourable Al/Ca ratios in soil moisture (Table 3.12), increasing K deficiency towards the stunted Mor-type forest and decreasing concentrations of total N in small roots and foliage (*cf.* Table 3.14).

Based on the high acidity and considerable concentrations of Al^{3+} in water extracted from the topsoil of the stunted Mor-type forests one would expect high Al concentrations in foliar and root tissues. However, Al was (much) higher in leaves and roots in the taller-statured Mull forests where it apparently does not have a toxic effect. Mull trees possibly immobilize Al by deposition in cell walls and vacuoles, where it is believed not to affect cell metabolism [*Cuenca et al.*, 1990]. Judging by their relatively low foliar concentrations of Al, Mor forest trees, on the other hand, seem to be unable to follow such a strategy. Instead, they apparently detoxify Al^{3+} by below-ground exudation of chelating compounds (including polyphenols) that form non-toxic organic-Al complexes, and by rhizosphere alkalinization. These strategies probably come at a high ecological cost [*Whipps and Lynch*, 1986], thus reducing the above-ground biomass increment of the forest. The processes behind these different strategies are unknown and require further study. A potentially fruitful line of research may be to investigate the sensitivity of Mor and Mull tree species to low pH and high Al^{3+} using seedlings grown in various nutrient solutions. Long-term effects could be studied by conducting field experiments that involve the adaptation of fine root dynamics to soil ameliorating measures. Because previous studies have demonstrated only moderate effects after (heavily) fertilization with N and P [*Tanner et al.*, 1990; *Stewart*, 1999], attention could now be focussed on ameliorating soil acidity by liming (alone or in combination with K) to a pH where concentrations of Al^{3+} in soil water are reduced to non-toxic levels [*cf.* *Cahn et al.*, 1993].

Table 3.14: Relative ranking of the four forest types on the basis of the nitrogen, aluminium, and polyphenol chemistry of their Ah soils horizons ($BaCl_2$-extractable NH_4^+), soil water (Al, NH_4^+, NO_3^-), small roots and foliage.

Soils (Ah horizons):							
Total N	MMor	>	PMull	>	WMull	>	Mor
$BaCl_2$-extractable NH_4^+	MMor	>	Mor	>	PMull	$\gtrsim$	WMull
Exchangeable Al^{3+}	MMor	>	PMull	>	Mor	>	WMull
Soil water (Ah horizons):							
NH_4^+, NO_3^-, pH	WMull	>	PMull	>	MMor	>	Mor
DON	Mor	>	MMor	$\gtrsim$	PMull	$\gg$	WMull
DOP	MMor	>	Mor	$\gg$	PMull	$\gg$	WMull
Phenols	Mor	>	MMor	$\gg$	WMull	>	PMull
Al^{3+}	Mor	>	MMor	>	WMull	>	PMull
Roots:							
Total N	WMull	$\gg$	PMull	$\gg$	Mor	=	MMor
Phenols	PMull	>	Mor	>	MMor	>	WMull
Al	WMull	>	PMull	$\gg$	MMor	$\gg$	Mor
K	WMull	>	PMull	>	MMor	>	Mor
Foliage:							
Total N*	WMull	>	Mor	$\gtrsim$	PMull	>	MMor
Phenols*	PMull	>	MMor	>	Mor	$\gg$	WMull
Phenols°	MMor	>	Mor	>	PMull	>	WMull
Al*°	WMull	>	MMor	>	PMull	$\gtrsim$	Mor
K*°	WMull	>	PMull	>	MMor	>	Mor
Litter:							
Phenols	PMull	>	WMull	>	MMor	>	Mor
Al	WMull	$\gg$	PMull	$\gtrsim$	MMor	>	Mor
K	WMull	$\gg$	PMull	>	MMor	>	Mor

*mature sunlit leaves as collected in December 1994 (Table 3.8); °old leaves (Table 3.4).

4

HYDROMETEOROLOGICAL OBSERVATIONS IN THE BLUE MOUNTAINS, JAMAICA, IN RELATION TO FOREST STATURE*

ABSTRACT

Precipitation inputs (both rainfall P and cloud water CW), global-, net- and photosynthetically active radiation (PAR), air temperature, relative humidity, wind speed and wind direction were recorded at Bellevue Peak (1849 m a.s.l.) in the Blue Mountains, Jamaica, throughout 1995 within the framework of a study of the causes of tropical montane forest stunting. In addition, amounts of CW intercepted by two nearby and almost adjacent montane forests of contrasting stature were estimated using various hydrological techniques. During the 365-day observation period, a total of 3060 mm of rain was recorded. Storms (median duration 0:57 h) were of low intensity (weighted mean: 4.1 $mm\,h^{-1}$). Amounts of CW intercepted by the nearby low-statured (main canopy height 5–8 m) ridge top forest were estimated at 3.4 % of corresponding P, whereas CW in the taller (7–12 m), less exposed forest was a mere 1.4 % of P. Such small differences in CW cannot be held responsible for the observed contrast in forest stature. Short-wave radiation inputs were reduced by 47 % by clouds compared to clear-sky conditions and amounted to c. 5040 $MJ\,m^{-2}$ over 1995 with typical daily totals of 11.9 and 15.2 $MJ\,m^{-2}$ during the winter (December–February) and summer months (June–August), respectively. However, intensities of PAR remained well above a level that would be limiting for photosynthesis during more than 80 % of relevant daytime hours (on average between 07:30 and 17:10 h), suggesting that low light conditions are not important in determining forest stature in the study area. During daytime hours, the vegetation experienced low saturation deficits (< 5 % of the mean saturated vapour pressure of 1.52 kPa) on 12 % of the days whereas deficits remained > 25 % for 13 % of the time. Penman open-water evaporation (E_0) ranged from 1.1 $mm\,d^{-1}$ during fully overcast conditions to 5.8 $mm\,d^{-1}$ on a cloudless day with an overall mean of 3.0 $mm\,d^{-1}$. As such, atmospheric evaporative demands are more than sufficient to enable adequate uptake of water and nutrients. Because there is no evidence that the forests suffer from severe droughts or prolonged waterlogging, it is concluded that other detrimental edaphic factors -notably high soil acidity, ex-

*With L. A. Bruijnzeel, R. A. M. de Jeu and N. J. Bink. Paper to be submitted in a slightly modified form to the *Caribbean Journal of Science*.

cess aluminium and low macro-nutrients (N, K)- are more likely to cause the observed contrasts in forest stature.

4.1 INTRODUCTION

Within the tropical montane forest zone a distinction is generally made between lower (in terms of elevational distribution, not tree height) montane rain forest (LMRF) and, usually shorter statured upper montane rain Forest (UMRF) [*Grubb*, 1977]. Apart from forest stature the chief differences in characteristics between the two forest types include, *inter alia*, tree density and dominant leaf size. *Grubb and Whitmore* [1966] suggested that LMRF had 'frequent' and UMRF 'long and persistent' cloud cover close to the ground although their statement was hardly quantified, whereas *Grubb* [1974] suggested that tall LMRF might also occur on fog-free locations. The idea that the frequency of fog and low cloud is the single most important factor determining the stature and type of tropical montane forest seems to be supported, at first sight, by numerous descriptive studies [reviewed by *Richards*, 1952; *Lamprecht*, 1958; *Stadtmüller*, 1987]. Generally speaking, the reductions in radiation load, air- and leaf temperatures and the increased cloudiness and humidity observed in montane areas compared to the lowlands, all tend to have an attenuating effect on transpiration and photosynthetic activity [*Grubb*, 1977; *Cavelier*, 1996; *Bruijnzeel and Veneklaas*, 1998]. As such, various attempts have been made to explain the distribution and physiognomy of montane forests in terms of concomitant changes in the chief meteorological variables with elevation [*e.g. Brown*, 1919; *Cavelier and Mejia*, 1990; *Bruijnzeel et al.*, 1993; *Pendry and Proctor*, 1996a]. Atmospheric evaporative demands, in particular, have been suggested to be reduced to such an extent that rates of water and nutrient uptake could be hampered [*Odum*, 1970; *Weaver et al.*, 1973; *Ash*, 1987].

Nevertheless, *Van Steenis* [1972] and *Tanner* [1977a] have shown that marked contrasts in stature may be observed between almost adjacent forests that are exposed to the same overall climatic conditions. Likewise, *Cavelier and Mejia* [1990] reported the occurrence of similarly statured forest on exposed ridge top and sheltered gully bottom sites on small islands in the Caribbean. Whilst this suggests that soil rather than climatic factors constitute the dominant reason for reduced forest stature on wet tropical mountains, the contradictory possibility remains that exposed summit and ridge top locations carrying stunted forest are not only likely to be more prone to water and nutrient stress due to their shallower soils [*Van Steenis*, 1972] but also potentially more efficient in catching atmospheric moisture and nutrients [*Stadtmüller*, 1987; *Asbury et al.*, 1994; *Clark et al.*, 1998]. The corresponding increase in duration of wet canopy conditions will not only lead to reduced transpiration [*Rutter*, 1967] but may in extreme cases also produce a chronic reduction in photosynthesis in some plants [*Ishibashi and Terashima*, 1995].

The difficulties associated with establishing and operating adequate weather

stations under the adverse topographic and climatic conditions prevailing in remote tropical montane terrain [*Baynton*, 1969; *Cavelier and Mejia*, 1990; *Bruijnzeel et al.*, 1993; *Hafkenscheid*, 1994; *Pendry and Proctor*, 1996b; *Clark et al.*, 1998] must be held responsible for the relative scarcity of quantitative hydrometeorological and soil hydrological information for tropical montane environments [*Bruijnzeel and Proctor*, 1995]. This hampers the testing of the various, sometimes mutually excluding, hypotheses that have been advanced to explain forest stature on wet tropical mountains. For instance, both excess soil water [*e.g. Hetsch and Hoheisel*, 1976] and moisture deficiency [*Werner*, 1988] have been proposed as a major factor in this regard (see reviews by *Bruijnzeel and Proctor* [1995]; *Cavelier* [1996]).

Within the framework of a larger programme that investigates the causes of forest stunting on wet tropical mountains, the hydrometeorology, soil hydrology, physiology, and biogeochemistry of two nearly adjacent montane rain forests of contrasting stature were studied at *c.* 1825 *m* in the Blue Mountains of Jamaica between January 1995 and April 1996. This paper reports on the prevailing climatic conditions in 1995; In addition, it quantifies the amounts of cloud water stripped by the two forests and discusses the influence of the respective climatic parameters on forest stature. The water budgets of the two study forests (including estimates of wet and dry canopy evaporation) are dealt with in Chapter 5.

4.2 Study area

4.2.1 Climate

If not stated otherwise, the following description of the (regional) climate is based on *National Meteorological Service of Jamaica* [1986]. The climate within the ESE-orientated Blue Mountain range (see Fig. 2.1 in Chapter 2) is strongly influenced by the northeasterly trade winds and the warm waters (25–28 °C) of the surrounding seas, with cold fronts migrating from the North American continent (between mid October and mid April) and tropical weather systems within the Caribbean region (depressions and hurricanes) occurring most frequently between April and December. Above 1,000 m elevation, Jamaica's tropical maritime climate (Köppen type A2m) gives way to a tropical montane climate (type Cfi). Annual rainfall in eastern Jamaica varies from less than 750 *mm* on the south coast to over 7000 *mm* on the northeastern (windward) slopes of the Blue Mountains (Fig. 2.1). Interpolation of the average isohyets suggests an annual rainfall of *c.* 2850 *mm* for the research area (Fig. 2.1). The nearest rainfall station is at Cinchona Botanical Gardens, which is situated at a distance of *c.* 3 *km* towards the SW at 1500 *m* a.s.l. and receives on average (1901–1990) *c.* 2275 $mm\,yr^{-1}$ (range 905–4464 $mm\,yr^{-1}$; J. R. Healey, *personal communication*). As such, the annual variability is large. Rainfall is also unevenly distributed over the year: October and November are normally very wet (>350 *mm* each) with a secondary peak in May and June, whereas March and July are relatively dry (<90 *mm* each; Fig. 4.1). Maximum rainfalls are generally associated with cold

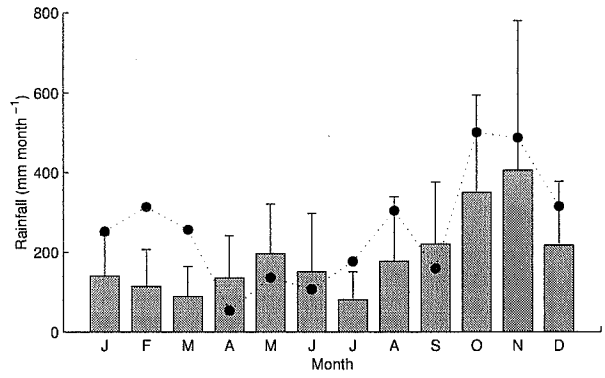

Figure 4.1: Long-term (1901–1990) average monthly rainfall (bars) at Cinchona (1500 *m* a.s.l.; J. R. Healey, *personal communication*) and monthly totals at Bellevue Peak (1849 *m* a.s.l.) in 1995 (circles). Vertical lines represent one standard deviation from the mean.

fronts migrating from North America during the winter months or with tropical storms during the late summer, with mean monthly totals exceeding 175 *mm* for the August–December period at Cinchona (maximum 2416 *mm* in November 1909; J. R. Healey, *personal communication*). Between 1901 and 1990, 15 % of all months at Cinchona had low rainfall (<50 *mm*) whereas only 1.4 % had rainfall totals of less than 10 *mm*. Showers at Cinchona are usually of short duration (approximately 1 *h*) and tend to fall in the mid-afternoon (*Shreve* [1914]; this study). Minimum rainfall occurs at night, suggesting convective rather than orographically induced rainfall.

Temperatures in the Blue Mountains depend mainly on elevation and are highest in June and August and lowest in December to February, though seasonal contrasts are moderate under the influence of the surrounding seas. Temperatures are strongly subject to the local orographic situation and show a regional mean lapse rate of *c.* 0.65 °*C* per 100 *m* rise in elevation. At Cinchona (1500 *m* a.s.l.), for example, average monthly maximum temperatures vary within 2 °*C* of the annual mean maximum temperature of 21.8 °*C vs.* 30.8 °*C* at the south coast (1951–1980; *National Meteorological Service of Jamaica* [1986]). Corresponding values for average monthly minimum temperatures are 13.5 °*C* and 24.0 °*C* respectively. During the year fluctuations of monthly averaged temperatures are small (<4 °*C* between the coldest and warmest month) but diurnal ranges can exceed 11 °*C* in the mountainous interior of the island. Mean monthly relative humidity at noon is close to 85 % (80–90 %) at Cinchona *vs.* 64 % (60–68 %) at the south coast, with relatively little seasonal variation.

Moisture-laden trade winds and day-time convection produce fog and low cloud, particularly on northerly (windward) slopes between 10:00 and 16:00 *h*, but rarely at night [*Shreve*, 1914]. Clouds develop first on the ridges and descend gradually towards the (leeward) coastal areas in the course of the afternoon. Monthly mean sunshine duration at Cinchona is 4.3 $h\,d^{-1}$ (range 3.9–5 $h\,d^{-1}$;

1951–1980; *National Meteorological Service of Jamaica* [1986]) compared to over 8 $h\,d^{-1}$ (7.1–8.8 $h\,d^{-1}$) for the southern coastal zone. Seasonal fluctuations in potential sunshine hours are limited, and range from 11.0 h in December to 13.2 h in June. At the southerly side of the Blue Mountains the prevailing trade winds have a persistently easterly to southeasterly direction (7.5–9 $m\,s^{-1}$ at sea level), but this can be influenced locally by land-sea wind interactions during daytime. Although outside the main track of tropical storms, Jamaica has been affected by 13 major hurricanes since 1871, on average once every 15 years [*Healey*, 1990; *Bellingham*, 1993]. Within the last 20 years, two major hurricanes, viz. Allen in 1980 and Gilbert in 1988, have passed Jamaica.

4.2.2 STUDY SITES

Although developed under largely similar geologic and climatic conditions, montane forests above *c.* 1300 m elevation in the Blue Mountains may show marked contrasts in stature, humus type and ecological functioning [*Tanner*, 1977a, 1980a, b, 1981]. Two nearly adjacent upper montane forest sites of contrasting stature were selected on a SW-orientated spur (18° 05' 29" N; 76° 38' 57" W) between Sir John Peak (1900 m a.s.l.) and Bellevue Peak (1849 m a.s.l.), the distance between the latter and the two sites being less than 150 m (Fig. 2.1).

The two forests are considered to represent intermediate stages in a sequence of four montane forest types with increasingly acid humus and topsoil (pH 4.4–3.0) and a gradual reduction in forest stature in a sequence of so-called 'well-developed' Mull forest (WMull, canopy height 12–17 m) to stunted Mor forest (5–7 m) as identified by *Tanner* [1977a, 1980b]. The shorter-statured forest of the two selected sites is situated on a ridge top (1824 m a.s.l.) and can be classified as 'moderately-developed' Mor forest (MMor, main canopy height 5–8 m) on the basis of its stature, species composition, epiphytic biomass and soil and humus type. The taller forest (7–12 m) is situated on a near-level slope section on the NW-side of the ridge at 1809 m a.s.l. and can be classified as 'poorly-developed' Mull forest (PMull), (E. V. J. Tanner, *personal communication*, 1995). Although the lateral distance between the sites is less than 30 m, the MMor site is more exposed to the prevailing winds (*cf.* Fig. 2.1) whereas the taller PMull forest is situated in a more sheltered position. Table 4.1 summarizes various basic structural characteristics of the two forests. A full description of their physiognomy, floristics, soils and biotics has been given in Chapter 2. Briefly, the principal species in the four forest types (WMull, PMull, MMor, and Mor) include *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, *Clethra occidentalis*, *Chaetocarpus globosus*, *Alchornea latifolia*, and *Podocarpus urbanii*. The species *L. octandra* is more numerous in Mor-type forests which also carry considerable numbers of *Clusia* cf. *havetioides*. On the other hand, *Clethra occidentalis*, *Podocarpus urbanii* and *Hedyosmum arborenscens* are more typical for the Mull-type forests [*Tanner*, 1977a, 1980a, b]. In the PMull forest, a discontinuous litter/fermentation layer plus a thin layer of humus overlie deep clay soils (fresh andesitic bedrock at > 3 m) whereas the siltier and shallower

Table 4.1: Species richness per site, total basal area (BA), tree height, density values for trees, the number of trees with multiple trunks (TWMT) and the trunk/tree ratios for trunks with diameter at breast height >5 *cm* for the PMull (area = 0.3 *ha*) and MMor (area = 0.24 *ha*) sites.

Forest	Species per site	BA $m^2\,ha^{-1}$	Height m	Trees	TWMT $no.\,ha^{-1}$	Trunk/tree ratio	LAI m^2m^{-2}
PMull	23	53.1	7–12	4400	567	1.19	5.0
MMor	10	44.4	5–8	6043	1043	1.29	4.1

($\leq$ 0.7 m) Mor forest soils have a thick ($\leq$ 0.5 m) layer of accumulated Mor humus and a well-developed surface root mat.

The development of the contrasting forest types in the area has received intensive study since the turn of the century, both in terms of floristics, productivity and biomass, foliar characteristics, and nutrient cycling [*Shreve*, 1914; *Grubb and Tanner*, 1976; *Tanner*, 1977a, 1980a, b, 1981, 1985; *Tanner and Kapos*, 1982], tree physiology [*Aylett*, 1985; *Kapos and Tanner*, 1985], forest nutrition [*Healey*, 1990; *Tanner et al.*, 1990], and effects of forest disturbance by hurricanes [*Bellingham*, 1993] or landslides [*Dalling*, 1992], but analyses of climatological conditions have focussed primarily on rainfall, temperature and humidity [*Shreve*, 1914; *Tanner*, 1980a, b, 1981; *Kapos and Tanner*, 1985].

Because of the limited areal extent of the contrasting forest types, it was not feasible to characterize climatic conditions separately above the two forests. Instead, a 12.5 m meteorological mast was erected above dense regenerating forest (main canopy height 3 m), with species similar to those found in the PMull and MMor forest sites, at nearby Bellevue Peak (1849 m, Fig. 2.1) to provide a continuous record of the respective climatic parameters. In view of the regional topography, the small lateral distance (150 m), the slight differences in altitude (25–40 m) and exposure to the prevailing winds, any differences in climatic conditions at Bellevue Peak and the two forest sites are believed to be very small (*cf.* Fig. 2.1). Although contrasts in roughness (aerodynamic resistance) between the three sites cannot be ruled out, the present observations are believed to be representative of above-canopy climatic conditions in the study area.

4.3 Instrumentation and methods

Rainfall (P, mm) at Bellevue Peak was measured at 3.5 m with a tipping bucket cum logger system (resolution 0.44 mm) manufactured at the Vrije Universiteit Amsterdam, backed by two manual gauges (100 cm^2 orifice) placed in a nearly adjacent clearing. The auto-recorded data were stored at 5-min intervals whereas the manual gauges were read every 3–4 days. From 21 July 1995 onwards, a manual rain gauge was also operated above the canopy of the MMor forest and read at 3–4 day intervals. Rainfall inputs measured by this gauge were virtually identical to those determined at Bellevue Peak.

Contributions by 'horizontal' precipitation (*HP*, *i.e.* cloud water plus wind-driven rain) at Bellevue Peak were recorded at 3.5 m using an identical tipping bucket system connected to a non-shielded 'Grünow'-type cylindrical fog gauge ($\oslash$ 10 cm, height 20 cm; mesh width 1 mm). Amounts of *HP* were evaluated by subtracting corresponding volumes of P from the catch of the fog gauge and dividing by the total area (628 cm^2) of the wire mesh cylinder [*Russell*, 1984]. One shielded (75 $\times$ 75 cm tarpaulin cover to reduce contributions by wind-driven rain) and one additional non-shielded manual fog gauge were installed in the adjacent clearing at 1.5 m above ground level and read every 3–4 days. The lateral distance between these gauges was less than 5 m. In addition, *HP* was measured above the MMor forest canopy, using non-shielded automated equipment identical to that used on Bellevue Peak. Throughfall (Tf) was measured in each forest with a tilted (30°) stainless steel gutter (400 $\times$ 4 cm) equipped with a tipping bucket cum logger device (0.3 mm per tip) in combination with twelve manual gauges (100 cm^2 orifice; 3–4 day sampling intervals) which were randomly located after sampling [*Lloyd and Marques-Filho*, 1988]. An areal average Tf volume was obtained by a weighted procedure taking the relative areas of the two types of gauges into account. Both gutters were cleaned every 3–4 days and treated regularly with a teflon solution to prevent blockage by organic debris and to minimize wetting losses. In each plot, twelve trees, representing a range of diameter classes, were fitted with rubber collars connected to 22.5 litre containers to measure stemflow (Sf). Gauges were emptied simultaneously with those for Tf while dividing Sf volumes by the projected area of the corresponding tree crowns enabled their expression in mm of water. It should be noted that analysis of the manually obtained data (P, Tf, Sf and *HP*) was restricted to the measurement interval (3–4 days), referred to in the following as 'periods', whereas the automatically recorded P and Tf data permitted analysis per precipitation event (referred to as 'events').

The observation mast was in operation from 1 January 1995 until 4 April 1996, with the exception of 28 July–21 October 1995, 16 November–15 December 1995 and 30 December 1995–16 January 1996 when parts of the equipment were damaged by excessive moisture (1996) or lightning strikes (1995). As some sensors (T, RH) could be replaced faster than others (wind speed, direction) data gaps differ for individual parameters. To improve the seasonal representativity of the data, this chapter is restricted to the observations made in 1995.

Short-wave radiation (R_s, Wm^{-2}) and net radiation (R_n, Wm^{-2}) were measured with a pyranometer (SP1110, Skye Instruments) and a net radiometer (Radiation and Energy Balance Systems Inc.) placed at 5.9 m on arms extending 1.5 m from the mast in such a way as to avoid shading of the instruments. Photosynthetically active radiation (PAR, wavelength range: 400–700 nm; $\mu mol\, m^{-2}\, s^{-1}$) was determined from the short-wave radiation records after calibrating half-hourly readings of a ceptometer (Delta-T Instruments) for a period of 10 days during which the ceptometer was installed directly adjacent to the mast. Measurements of below-canopy PAR (Q_i) were taken at breast height in the two forest plots between 11:00 and 13:00 h under clear-sky conditions to obtain the degree of PAR attenuation by the canopy. A sample for a single position within each forest consisted of the average of 12 individual readings taken

at 30° intervals within a full circle. During these measurements the readings of corresponding total incoming (above-canopy) PAR (Q_0) were taken at regular intervals (15–20 *min*) in an adjacent clearing. Eighty and 48 samples were taken in the PMull and MMor forests, respectively. The values of below-canopy and total incoming PAR were used to compute the leaf area index (LAI, m^2m^{-2}) using the Beer-Lambert equation:

$$LAI = \frac{-ln\left(\frac{Q_i}{Q_o}\right)}{k} \tag{4.1}$$

where k is the canopy light extinction coefficient, an empirical parameter depending on the geometry of the canopy. When using Eq. 4.1, a random distribution of foliage and leaf orientation has to be assumed. Although this is often not the case in practice, Eq. 4.1 has been demonstrated to be rather insensitive to violations of this assumption [*Jarvis and Leverenz*, 1983; *Pierce and Running*, 1988].

Net soil heat fluxes (G_s, Wm^{-2}) were determined with a soil heat flux plate (Middleton & Co.) placed underneath a *c.* 5 cm thick litter layer at Bellevue Peak. Care was taken to avoid disturbance of the litter layer during installation. Air temperature (T, °C) and relative humidity (RH, percentage of saturation) were measured at 3.5 m with a precision thermometer (Campbell Sci. HMP 35AC) and a Vaisala capacitative humidity sensor after 60 s of forced ventilation (at approximately 2 $m\,s^{-1}$). Both sensors were placed in a Gill-type radiation shield to protect them against direct insolation and rainfall. The accuracy of the thermometer was typically 0.1 °C. The accuracy of the RH sensor was typically better than 2 % whereas a long-term stable precision of less than 1 % per year was stated by the manufacturer. Above 97 % RH, condensation on the sensor could occur and the sensor would lose its normal accuracy. Relative humidity readings in excess of 100 %, as recorded sometimes during periods of prolonged wetness, were set at 100 %. Both T and RH sensors were regularly calibrated against readings with an Assmann psychrometer. Wind direction was measured using a potentiometer windvane (Vector Instruments, W200P) placed at 12.5 m. Wind speeds were determined at three heights (5.94, 7.65, and 10.1 m) using three-cup anemometers (Vector Instruments, A101M/L), supported by arms (0.5 m) orientated towards the prevalent wind direction (ESE). The sensors had a stalling speed of 0.15 $m\,s^{-1}$ and an accuracy of 1–2 %. All instruments were sampled at 30-s intervals except for the T and RH probes (every 5 *min*). Data were processed by a Campbell 21X data logger system. Averages and standard deviations were calculated over 30-*min* periods and stored using solid-state memory boxes.

4.4 Results

4.4.1 Gross and net rainfall

In total, 3060 *mm* of rainfall was measured by the manual gauges at Bellevue Peak between 1 January and 31 December 1995, *i.e.* about 7 % above the

estimated average annual rainfall for the research area (2850 *mm*; *cf.* Fig. 2.1) and *c.* 25 % above the long-term (1901–1990) mean annual rainfall record for nearby Cinchona (2275 $mm\,yr^{-1}$). Monthly rainfall at Bellevue Peak in 1995 generally exceeded the corresponding long-term averages for Cinchona, except for the April–June period and September, which were somewhat drier (Fig. 4.1).

The automated equipment identified 327 separate events distributed over 205 days with rain in excess of 0.44 *mm*, with an average of 14.9 *mm* per rain day. The 327 separate events represented a total duration of 727 *h* of rainfall (or 8.3 % of total time). Extending the duration of each storm larger than 1 *mm* (n = 197) by 2 *h* to allow for the complete evaporation of water from the wet vegetation at the end of the storm [*cf. Hafkenscheid et al.*, 1998] suggested a total of 1121 *h* (12.8 % of total time) during which the canopy was likely to be wet by rain. A total of 71 dry periods of 24 hours or more were recorded (160 dry days in total, mean duration 2.3 days) of which 51 (72 %) were less than 48 hours. The longest continuously dry period lasted 11 days (27 March to 6 April). Average values for storm size, duration and intensity were 9.41 *mm*, 02:13 *h*, and 5.12 $mm\,h^{-1}$ (weighted mean: 3060 *mm* divided by 727 *h* or 4.2 $mm\,h^{-1}$), respectively. However, the highly skewed frequency distributions of these parameters require the use of median rather than mean values. The corresponding median values were 1.78 *mm*, 0:40 *h*, and 2.36 $mm\,h^{-1}$, respectively (Table 4.2). Forty percent (n = 131) of the events were <1 *mm* (representing 2.5 % of total P), whereas 4.3 % (n = 14) of the events delivered >50 *mm* each (44.4 % of total P). Rainfall intensities were low: 7 % of the storms had an average intensity (total amount of a single storm divided by its duration) of $\leq$1 $mm\,h^{-1}$; 47 % showed intensities $\leq$ 2 $mm\,h^{-1}$ whereas only 11.3 % of the storms had an intensity >10 $mm\,h^{-1}$. Showers tend to fall in the afternoon (Fig. 4.2), with *c.* 65 % of the rainfall occurring during daytime hours (06:00 – 18:00 *h*). Minimum rain falls in the late evening, suggesting the rain to be convective rather than orographic.

The net precipitation components for 1995 amounted to 2233 *mm* for *Tf* in the PMull forest *vs.* 1821 *mm* in the MMor forest (73.0 % and 59.5 % of corresponding P) and to 399 and 559 *mm* (11.1 and 18.3 % of P) for *Sf* in the PMull and MMor forest, respectively. The correlation between the continuously recorded and the spatially averaged manual data was modest ($r^2 \leq 0.75$), largely as a result of frequently occurring drip points [*cf. Lloyd and Marques-Filho*, 1988]. Auto-recorded data were available for 257 and 307 days in the PMull and MMor sites, respectively. The corresponding means and median values for amount, duration and intensity of throughfall events in the two forests are given in Table 4.2. Similar data for stemflow are not available as the latter was only obtained manually at 3–4 day intervals.

4.4.2 Cloud water deposition

The two non-shielded fog gauges at Bellevue Peak registered a surplus over P of 0.1 % (in clearing at 1.5 *m*) and 22 % (in mast at 3.5 *m*) whereas the non-shielded gauge above the MMor forest suggested 12 % extra precipitation. By contrast,

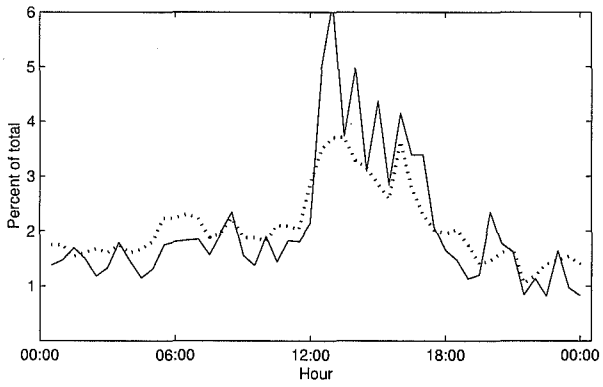

Figure 4.2: Diurnal distribution (at half-hourly intervals) of relative amounts (solid line) and the relative frequency of occurrence (dotted line) of rainfall at Bellevue Peak in 1995.

Table 4.2: Average and median size, duration, and intensity of rainfall- (at Bellevue Peak) and throughfall events (at the MMor and PMull sites) during 1995. The number of days represents the actual time that the recoding gauge were functioning.

	Number of		Mean values			Median values		
Site	Days	Events	Size	Duration	Intensity	Size	Duration	Intensity
			mm	h	$mm\,h^{-1}$	mm	h	$mm\,h^{-1}$
P_{Bellevue}	365	327	9.41	02:13	5.12	1.78	00:40	2.36
Tf_{MMor}	307	217	6.27	02:35	2.67	1.19	00:40	1.19
Tf_{Pmull}	257	159	6.75	03:23	1.61	0.94	01:20	0.62

the covered fog gauge in the clearing gave a value of 6.4 % (197 mm). These variable results demonstrate that estimations of cloud water incidence (CW) based on the subtraction of large amounts of P from (P+HP) are problematic when non-shielded (Grünow-type) gauges are exposed to wind-driven rain [*cf. Schemenauer and Cereceda*, 1994]. They also illustrate the strong influence of gauge exposure [*cf. Schellekens et al.*, 1998].

Amounts of cloud water 'intercepted' by the vegetation of the two forest sites are likely to differ from those estimated using a simple fog gauge. *Hafkenscheid et al.* [1998] compared various approaches to quantify the amounts of cloud water interception by the stunted MMor site. The present analysis includes both study sites, using a slightly different data set.

The first approach involved comparison of (linear) relationships between precipitation components (P, Tf) for events with or without fog [*cf. Harr*, 1982], assuming conditions to be fog-free whenever the shielded 'Grünow' gauge readings were less than 1 % of P. Although the regression equations generally had quite acceptable coefficients of determination (Table 4.3), the differences in slope were not significant at the 95 % probability level, rendering the results meaningless from the statistical point of view. Taking the regression lines at face

value, the extra Tf generated by fog would be 55 and 194 mm for the MMor and PMull, respectively, or 3.2 and 11.8 % of the corresponding P. Similar results were obtained using the manually measured $Tf+Sf$ data (3–4 day periods) (Table 4.3). The fact that the most sheltered forest of the two (PMull) gave the higest fog incidence indicatess the limitations of this 'throughfall correlation method' under the prevailing conditions [*cf. Hafkenscheid et al.*, 1998]. Therefore, another approach was followed as well. Based on the assumption that all Tf recorded after the last registration of P had to be generated by CW, and applying a threshold of 2 h to eliminate residual rainfall-induced crown drip [*Schellekens et al.*, 1998], a total of 93 mm of additional Tf was determined for the MMor forest during those rain-free periods for which simultaneous recordings of Tf and HP were available. This amount may be taken to represent CW contributions only and equals 3.4 % of the total rainfall associated with the preceding storms. For the less-exposed PMull the corresponding values read 31 mm and 1.4 % of P, respectively. When these percentages are extrapolated to a one-year period, CW would amount to 43 $mm\,yr^{-1}$ at the PMull *vs.* 104 $mm\,yr^{-1}$ at the MMor.

Table 4.3: Statistics of linear regressions between rainfall (P) and throughfall (Tf) for *events* and 3–4 day *periods* (Tf, Tf + stemflow Sf) during conditions with and without fog in the stunted (MMor) and tall (PMull) forest sites. Data for which P exceeded 100 mm were excluded from the analysis to improve comparability of the respective data sets.

Condition	Statistics	Tf–P_{events}		Tf–$P_{periods}$		$(Tf+Sf)$–$P_{periods}$	
		MMor	PMull	MMor	PMull	MMor	PMull
Fog-free	slope	0.639	0.509	0.573	0.735	0.776	0.856
	n	30	18	33	33	32	33
	r^2	0.891	0.965	0.904	0.949	0.902	0.945
With fog	slope	0.658	0.656	0.621	0.815	0.828	0.975
	n	155	133	76	79	76	75
	r^2	0.805	0.886	0.865	0.854	0.882	0.875

4.4.3 Seasonal and diurnal patterns of other climatic variables

Monthly averages of mean daily values of global (7.3 m) and net radiation (5.9 m), soil heat flux, temperature and relative humidity (3.5 m), and wind speed at 10.1 m as observed between 1 January and 31 December 1995 are presented in Fig. 4.3. The mean diurnal ranges of the same variables are displayed in Fig. 4.4, together with those for averaged bright and cloudy conditions (n = 20 days each), as selected throughout the observation period on the basis of daily radiation loads. Such cloudy (highest short-wave radiation input R_s: 3.3 $MJ\,m^{-2}\,d^{-1}$) and sunny conditions (lowest R_s: 25.8 $MJ\,m^{-2}\,d^{-1}$) represented *c.* 10 % of the total time during which the mast was in operation.

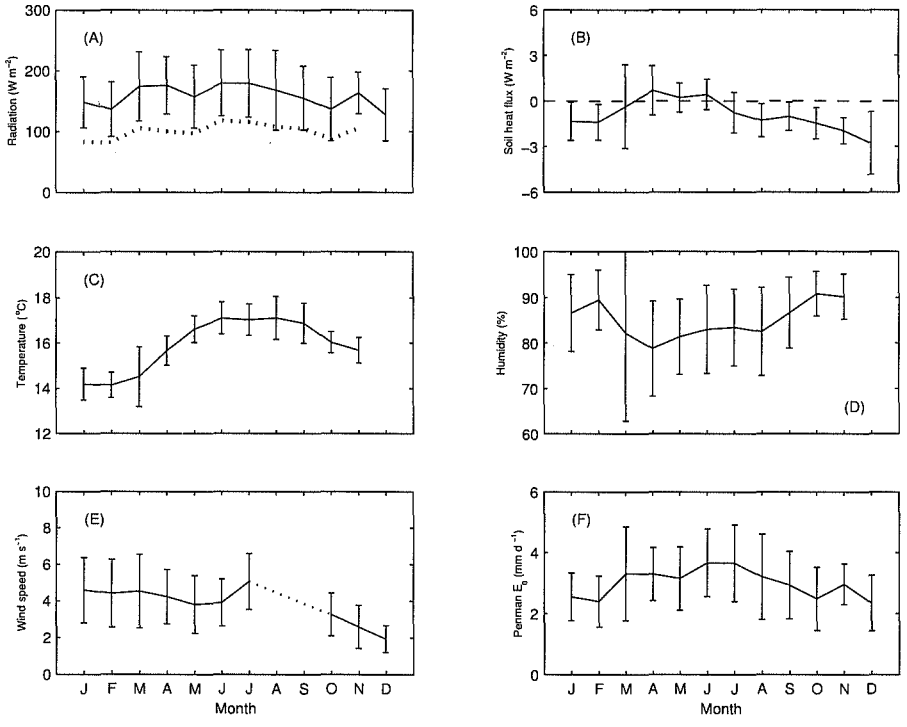

Figure 4.3: Seasonal course (monthly averages of daily means) of (A) short-wave (solid line)- and net radiation (dotted line, Wm^{-2}), (B) soil heat flux (Wm^{-2}), (C) air temperature ($^{\circ}C$), (D) relative humidity (%), (E) wind speed at 10.1 m (ms^{-1}), and (F) Penman open-water evaporation (E_0, $mm\,d^{-1}$) between 1 January and 31 December 1995 at Bellevue Peak (1849 m a.s.l.). Vertical lines represent ± one standard deviation.

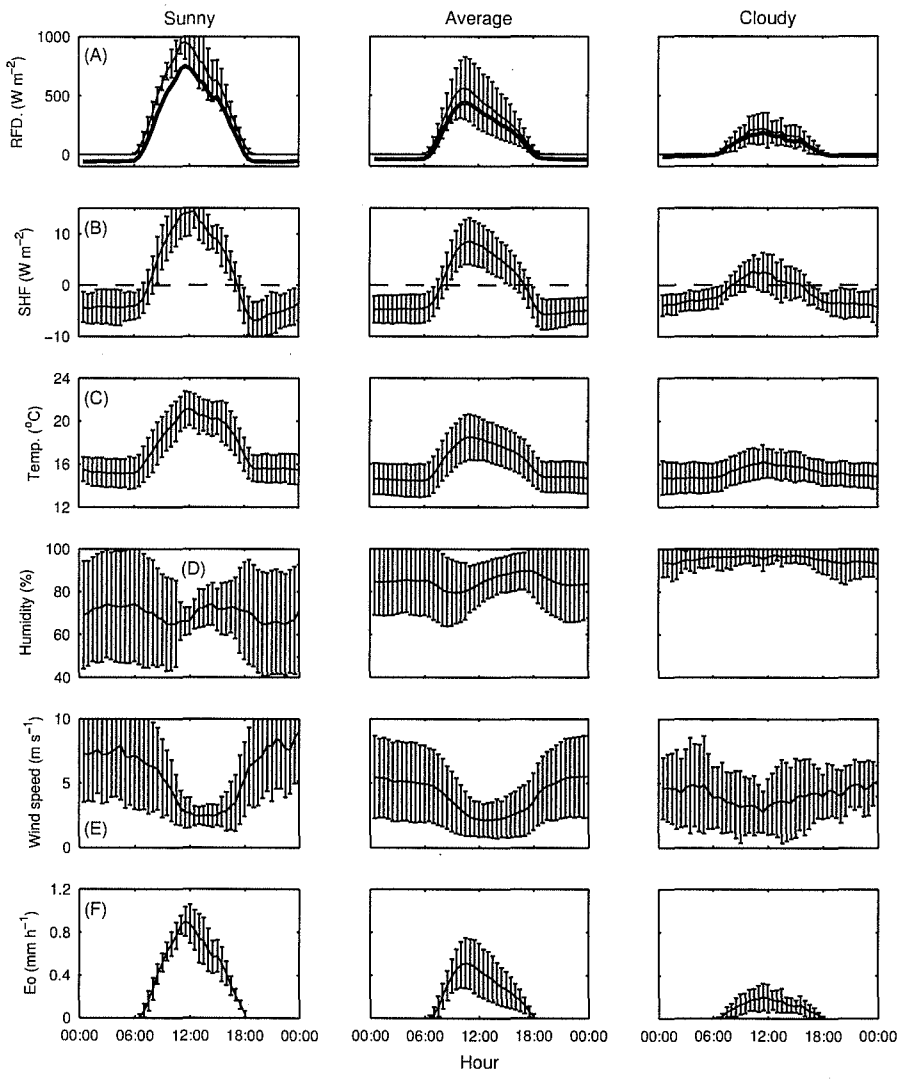

Figure 4.4: Averaged diurnal patterns for (A) radiation flux densities (RFD, Wm^{-2}) of actual short-wave radiation (normal line) and net radiation (bold line), (B) soil heat flux (SHF, Wm^{-2}), (C) air temperature ($°C$), (D) relative humidity (%), (E) wind speed at 10.1 m ($m\,s^{-1}$), and (F) Penman open-water evaporation (E_0, $mm\,d^{-1}$) between 1 January and 31 December 1995 at Bellevue Peak (1849 m a.s.l.). Corresponding averaged patterns for selected clear-sky and overcast conditions (n = 20 days each) have been added for comparison. Vertical lines represent ± one standard deviation.

Global radiation

The mean daily short-wave radiation input (R_s) was 13.8 ± 4.6 $MJ\,m^{-2}$ (range 2.9–27.0 $MJ\,m^{-2}$; n = 318) with relatively minor seasonal fluctuation (Fig. 4.3A). To assess the reduction in R_s due to the presence of a cloud cover, idealized diurnal patterns were constructed from the highest half-hourly readings available for each month and compared to actually measured values. Deviation of the former from modelled potential radiation flux densities based on latitude, longitude, and time of year (R_{pot}; *Oke* [1987]) were less than 7 %. Actually measured R_s was within 95 % of the potential value during 4 days only and less than 50 % on 145 out of 318 days. An average reduction of 47 ± 18 % compared to potential values was derived. An examination of the diurnal patterns of R_s (Fig. 4.4A) shows that intensities, compared to clear-sky conditions, were reduced by 77 % under fully overcast conditions. Average daily loads for sunny and overcast conditions were 24.0 and 5.6 $MJ\,m^{-2}$, respectively. Cloud-induced reduction of R_s was most profound between 12:30 and 16:30 h when, on average, attenuation was over 55 % compared to potential levels whereas the reduction was less than 35 % between 07:30 and 10:30 h (Fig. 4.4A).

Net radiation

Mean daily net radiation (R_n) was 100.2 ± 34.5 Wm^{-2} (8.65 $MJ\,m^{-2}\,d^{-1}$) or 63 % of the corresponding value of R_s (Fig. 4.3A), although maximum intensities of *c.* 750 Wm^{-2} were attained during bright days (Fig. 4.4A). Linear regression analysis was applied to the half-hourly and averaged daily data pairs for R_s and R_n (all in Wm^{-2}). For conditions with $R_s > 50\ Wm^{-2}$ (half-hourly data only) the resulting expression reads:

$$R_n = 0.778_{(\pm 0.002)} \cdot R_s - 11.12_{(\pm 0.75)} \quad r^2 = 0.97 \quad n = 6417 \tag{4.2}$$

whereas for daily (24-h) values it is given by:

$$R_n = 0.606_{(\pm 0.014)} \cdot R_s + 2.57_{(\pm 2.39)} \quad r^2 = 0.86 \quad n = 304 \tag{4.3}$$

The average daytime net radiation (10.45 $MJ\,m^{-2}$) was about 74 % of R_s during clear-sky conditions, increasing to 81 % during overcast conditions (Fig. 4.4A). On average, daytime values for R_n were 5.9 times the upward flux during nighttime which was typically $-1.78\ MJ\,m^{-2}$ (mean intensity $-39.7\ Wm^{-2}$). Comparing sunny and cloudy conditions (Fig. 4.4A), the reduction in positive daytime fluxes of R_n due to clouds can be as much as 82 % (17.72 *vs.* 4.47 $MJ\,m^{-2}$). Corresponding values for nights that precede or succeed days with clear-sky conditions (and therefore likely to be relatively free of clouds themselves) and nights that precede or follow overcast days were -2.56 and $-0.68\ MJ\,m^{-2}$, respectively, clearly illustrating the increase in eradiation during cloudless nights.

The albedo (α) of the regenerating forest around the observation mast was estimated for 295 half-hourly periods between 30 August and 12 September 1995, using simultaneous observations of upward short-wave radiation ($R_s\uparrow$, inverted pyranometer readings) and downward short-wave radiation (R_s) as obtained from R_n readings and Eq. 4.2. The analysis was limited to values of

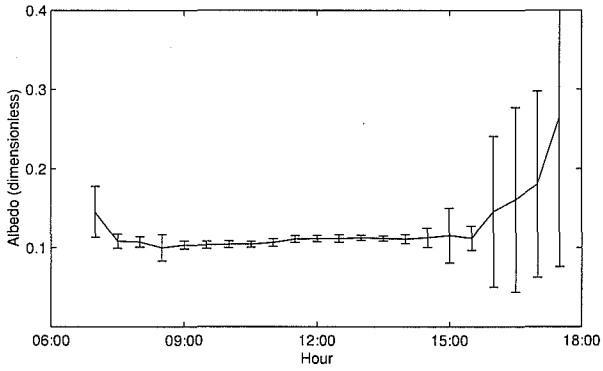

Figure 4.5: Averaged diurnal pattern of the solar radiation reflection coefficient (albedo) as observed above regenerating forest at Bellevue Peak (1849 *m* a.s.l.) between 30 August and 12 September 1995. Vertical lines represent ± one standard deviation.

$R_s \uparrow$ and modelled R_s in excess of 1 Wm^{-2} and 20 Wm^{-2}, respectively. The diurnal course of α was remarkably constant throughout much of the day at 0.109 ± 0.012 (07:30–15:30 *h*; n = 231), only to increase sharply after 15:30 *h* (Fig. 4.5). The reflection of short-wave radiation was clearly reduced (α = 0.076 ± 0.012; n = 13 half hours) during times when rainfall was recorded (not shown).

Photosynthetically active radiation (PAR)

For values of R_s >25 Wm^{-2}, PAR was related to short-wave radiation R_s according to:

$$PAR = -1.68E^{-4}.R_s^2 + 2.09.R_s \quad r^2 = 0.98 \quad n = 262 \tag{4.4}$$

where PAR is in $\mu mol\, m^{-2}\, s^{-1}$ and R_s in Wm^{-2}. The ratio PAR / R_s equalled 2.0 when a simple linear relationship that included all half-hourly data was forced through the origin (r^2 = 0.98; n = 307). Average daytime (06:00–18:00 *h*) PAR at Bellevue Peak was estimated from the R_s record and Eq. 4.4 at 650 $\mu mol\, m^{-2}\, d^{-1}$ (range 140–1,241 $\mu mol\, m^{-2}\, s^{-1}$). Compared to the potential radiant flux density equivalent of 1,272 $\mu mol\, m^{-2}\, s^{-1}$, the effect of the presence of clouds on PAR levels was a reduction of 51 % on average whereas a reduction of 77 % in R_s was obtained when comparing selected sunny- with fully overcast conditions (*cf.* Fig. 4.4A).

At the MMor site, the below-canopy PAR (Q_i) ranged from 38 to 1,134 $\mu mol\, m^{-2}\, s^{-1}$ (average: 276 ± 223 or 13 % of incoming PAR; n = 48 sample positions) *vs.* 8–430 $\mu mol\, m^{-2}\, s^{-1}$ (average: 101 ± 86 or 5 % of incoming PAR, n = 80 samples) below the PMull forest canopy. These differences clearly reflect the more open character of the MMor forest. The mid-day value of the PAR arriving at the top of the canopy was *c.* 2,070 $\mu mol\, m^{-2}\, s^{-1}$ as measured in a nearby clearing.

The values of below-canopy and total incoming PAR may be used to compute the leaf area index (LAI) using the Beer-Lambert equation for light transmittance through vegetation canopies [*Lang*, 1987] (Eq. 4.1). The light-extinction coefficient k ranges from 0.3 to 1.5, with the lower values corresponding with erectophyl canopy types [*Ross*, 1975]. Few data are available for tropical rain forest in general whereas information for montane forests seems to be entirely absent. *Kira* [1978] found $k = 0.7$ for tall lowland forest in Malaysia. An extinction coefficient of 0.5 was therefore believed to be a representative estimate for the rather open, short-statured MMor forest. This gave an LAI value of 4.0 m^2m^{-2}, *i.e.* almost identical to the 4.1 m^2m^{-2} obtained using data on annual leaf fall and specific leaf area (*cf.* Section 2.3.1). Based on the physiognomic contrast between the MMor and PMull forests a k value of 0.6 is probably more appropriate for the taller PMull forest. Solving Eq. 4.1 for the PMull forest resulted in an LAI of 5.0 m^2m^{-2}, which is not only much higher but also more plausible a value compared to the estimate based on leaf fall and specific leaf area (3.4 m^2m^{-2}; see Section 2.3.1 for more details).

Soil heat flux

During the 305 days of observations of the net soil heat flux (G_s), a net negative (upward) value of $-18.94\ MJ\,m^{-2}$ passed the litter layer, corresponding to a daily average value of $-0.72 \pm 1.69\ Wm^{-2}$. As such, a distinct loss of energy occurred from the soil, particularly in January and February 1995 and from July onwards (Fig. 4.3B). The diurnal pattern consisted of an average positive (*i.e.* downward) flux between 08:00 and 17:00 h of 177 $kJ\,m^{-2}$ (5.16 Wm^{-2}) whereas on average $-239\ kJ\,m^{-2}$ ($-4.58\ Wm^{-2}$) was lost to the atmosphere at night (Fig. 4.4B). Maximum and minimum daily intensities were $+7.4\ Wm^{-2}$ and $-8.0\ Wm^{-2}$, respectively. During sunny days, G_s was positive (downward) between 08:00 and 17:15 with an average flux of 314 $kJ\,m^{-2}$ whereas $-229\ kJ\,m^{-2}$ was lost during the nights prior to and following sunny days. Corresponding maximum and minimum intensities were +14.5 and $-6.8\ Wm^{-2}$, respectively (Fig. 4.4B). Under cloudy conditions, soil heat fluxes were positive for less than 6 h, starting around 08:10 h and already reversing their sign around 15:40 h (Fig. 4.4B). The magnitude of positive G_s during cloudy days (at a mean value of $+36.7\ kJ\,m^{-2}$) was only 11.7 % of the value observed for sunny conditions whereas the outward flux (mean value $-178\ kJ\,m^{-2}$) was 77.7 % of that associated with non-cloudy conditions. Compared to the average clear-sky values for R_s, daytime G_s was less than 1.4 % on average, dropping to 0.78 % during cloudy conditions. Average nighttime G_s was *c.* 16 % of corresponding R_n ($-1.48\ MJ\,m^{-2}$), implying that an additional 84 % (1.24 $MJ\,m^{-2}$) of heat must be lost from the vegetation, the air column between the vegetation, and the top of the litter layer.

Temperature and humidity

Average (24 h) above-canopy air temperature (T) was 15.9 ± 1.4 °C (n = 316 days) whereas the average relative humidity (RH) was 84.8 ± 10.4 % (n = 304 days). The corresponding mean values for daytime hours (06:00 – 18:00 h) were 17.1 ± 1.5 °C and 84.8 ± 9.0 %, respectively. Although temperatures showed a distinct seasonal pattern (Fig. 4.3D), no such distribution was evident for RH whose values were generally maintained between 80 and 90 % around the year (Fig. 4.4C). The average diurnal pattern of T closely followed that of R_s (*cf.* Fig. 4.4A), with the mean maximum temperature (18 °C) typically being reached around 11:00 h, after which T decreased gradually until *c.* 19:00 h (Fig. 4.4C). Night-time (21:30 – 06:00 h) cooling was generally less than 0.4 °C, with the minimum value being reached around daybreak (*c.* 06:00 h). Under sunny conditions, T remained above 20 °C between 10:30 and 15:30, followed by a rapid decline, whereas for cloudy conditions fluctuations of T were very limited (Fig. 4.4C).

Patterns of RH showed comparatively little fluctuation throughout the day, with values around 70 % (for clear-sky conditions), 85 % (average conditions) or 95 % (cloudy conditions) depending on radiation loads (Fig. 4.4D). During sunny conditions, RH dropped during the first 3.5 h after daybreak and again for about two hours after sunset, although values hardly got below 75 %. During cloudy conditions, however, RH remained close to saturation for most of the day (Fig. 4.4D). On average, RH was lowest in the first half of the morning after which it increased steadily to a value of *c.* 90 % in the late afternoon. Such a pattern is conform to the typical clear mornings and clouded afternoons observed in the area (*Shreve* [1914]; *cf.* Fig. 4.4A).

Wind speed and direction

Average daily wind speeds at 10.1 m were typically between 4 and 5 $m\,s^{-1}$ during the first half of the year but distinctly lower (2–3 $m\,s^{-1}$) after measurements were resumed in October. Maximum average wind speed was observed in July (Fig. 4.3E). The overall mean daily wind speed was 4.1 ± 1.8 $m\,s^{-1}$ (n = 204 days), with daytime values of 3.1 ± 1.4 $m\,s^{-1}$ (maximum: 9.4 $m\,s^{-1}$) increasing to 5.2 ± 2.3 $m\,s^{-1}$ (maximum: 13.9 $m\,s^{-1}$) at night (Fig. 4.4E). An interesting pattern was revealed by comparing above-canopy wind speeds for clear-sky and overcast conditions. On sunny days, the average wind speed increased to 5.8 $m\,s^{-1}$, with a daytime minimum of 2.4 $m\,s^{-1}$ and a nocturnal maximum of 9.0 $m\,s^{-1}$. Conversely, during cloudy conditions there was much less diurnal fluctuation around the mean value of 4.1 $m\,s^{-1}$ (2.8–5.2 $m\,s^{-1}$; Fig. 4.4E). The all-time maximum half-hourly wind speed was 16.4 $m\,s^{-1}$ (recorded on 16 February 1995) although in view of the corresponding standard deviation, individual gusts probably exceeded 20 $m\,s^{-1}$. Wind direction was typically ESE, especially during the night when the scatter observed during the daytime was drastically reduced.

Reference evaporation rate

A convenient measure to characterize overall climatological conditions at a location is the rate of open-water evaporation E_0 [*Penman*, 1956]. Although the original formula requires all parameters to be measured above short grass at a height of 2 m, the present observations were made at 3.5 m above a regenerating forest (RH, T), with the wind speed as measured at 5.94 m converted to that for 3.5 m using a logarithmic wind profile [*Thom*, 1975]. Instrumental failure reduced the number of days for which E_0 could be computed directly to 233 (Fig. 4.6). The corresponding mean E_0 was 3.1 ± 1.1 $mm\,d^{-1}$ (range: 0.7–8.4 $mm\,d^{-1}$). However, a good relationship was found between daily values of E_0 (in $mm\,d^{-1}$) and R_s (in Wm^{-2}):

$$E_0 = -0.3651 + 0.0212.R_s \quad r^2 = 0.91 \quad n = 233 \tag{4.5}$$

The use of Eq. 4.5 allowed the data set for E_0 to be increased to 318 days. The resulting mean daily open-water evaporation rate (Fig. 4.6) was 3.0 ± 1.2 $mm\,d^{-1}$ (range: 0.4–8.4 $mm\,d^{-1}$; n = 318), with 83 % of the days exhibiting rates of 2 $mm\,d^{-1}$ or more. For 1995, the incident rainfall (3060 mm) exceeded E_0 (extrapolated to 1 year: 1104 mm) by a factor of 2.8. The overall average value of 3.0 $mm\,d^{-1}$ represents a reduction of 48 % compared to that for cloudless conditions (5.8 $mm\,d^{-1}$) whereas for fully cloudy days E_0 was reduced by 81 % to a value of 1.1 $mm\,d^{-1}$(Fig. 4.4F). Even more so than in the case of temperature, diurnal patterns of E_0 (Fig. 4.4C,F) are nearly identical to those for R_s (Fig. 4.4A). On a diurnal basis, average hourly reference evaporation rates were 0.15 $mm\,h^{-1}$, with average maximum intensities (0.52 $mm\,h^{-1}$) being reached around 10:30 h. On sunny days the mean hourly E_0 was 0.20 $mm\,h^{-1}$, increasing towards 0.9 $mm\,h^{-1}$ around midday. Conversely, during days with clouds, maximum intensities of E_0 hardly exceeded 0.2 $mm\,h^{-1}$, with mean hourly rates of evaporation close to 0.06 $mm\,h^{-1}$ (Fig. 4.4F).

4.5 Discussion

In the following the various effects on forest stature caused by the climatic conditions prevailing on wet tropical mountains in general and in the study area in particular are examined.

4.5.1 Reduced radiation and photosynthesis

Although radiation in the mountainous interior of Jamaica is evidently reduced compared to that in the lowlands, and although radiant energy during conditions of low cloud is reduced by nearly 80 % compared to clear-sky observations (Fig. 4.4A), the overall attenuating effect is not very pronounced. The estimated reduction in annual radiation load from the coast to an elevation of *c.* 1600 m a.s.l. in the study area (16 %; *Aylett* [1985]) falls at the low end of the 15–50 % range in reductions reported for tropical montane forests [*Bruijnzeel and Veneklaas*, 1998] and is similar to the 15% observed for the island of Rakata, Indonesia where radiation loads at sea level and above stunted cloud forest at 700

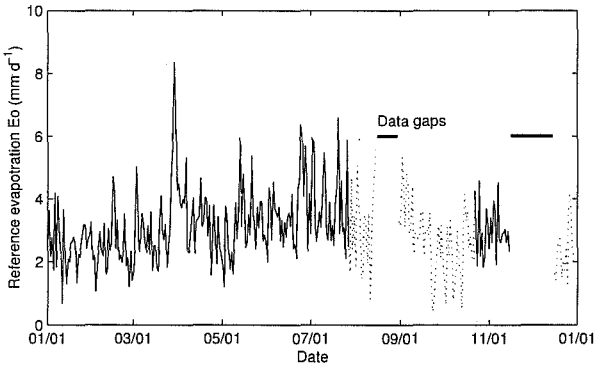

Figure 4.6: Daily totals of open-water reference evaporation at Bellevue Peak (1849 *m* a.s.l.) as determined with the Penman evaporation model [*Penman*, 1956] for 233 days (solid line) and a linear regression equation (Eq. 4.5) between E_0 and short-wave radiation (R_s) for 85 additional days (dotted line).

m a.s.l. were compared [*Hafkenscheid*, 1994]. The presently recorded average solar radiation total of 13.8 $MJ\,m^{-2}\,d^{-1}$ (n = 318 days) is very similar to the mean intensity experienced by 15 *m* tall 'mossy' forest at 885 *m* in East Malaysia (13.4 $MJ\,m^{-2}\,d^{-1}$; *Bruijnzeel et al.* [1993]) where the development of a daily cloud cap reduced radiant energy by 35 % (compared to that recorded at sea level) at an elevation less than half that of the present sites. The present total of R_s is also nearly identical to the 13.9 $MJ\,m^{-2}\,d^{-1}$ reported by *Holwerda* [1997] above 25 *m* tall colline (Tabunuco) forest at 265 *m* in the Luquillo Mountains, eastern Puerto Rico. Conversely, a 2–3 *m* high 'elfin' cloud forest at Pico del Este (1015 *m*) in Puerto Rico only received 7.7 $MJ\,m^{-2}\,d^{-1}$, implying a reduction in radiation load of 45 % between 265 and 1015 *m* [*Holwerda*, 1997]. Earlier, *Baynton* [1969] had obtained an average value of 11.0 $MJ\,m^{-2}\,d^{-1}$ during a one-year observation period at nearby Pico del Oeste (1050 *m* a.s.l.). Therefore, although the presence of low cloud and fog has a substantial effect on the light climate at the study sites on individual days (*cf.* Fig. 4.4A), the overall radiation loads are apparently sufficient to enable the development of tall-statured forest at other locations.

The capacity of the photosynthetic apparatus of tropical montane trees is known to be not systematically lower than that of lowland forests [*Bruijnzeel and Veneklaas*, 1998]. Light levels required for full photosynthetic activity of rain forest vegetation range from 200 to 600 $\mu mol\,m^{-2}\,s^{-1}$ [*Pearcy and Calkin*, 1983; *Chazdon*, 1986; *Pearcy*, 1987; *Hogan*, 1988] whereas *Aylett* [1985] reported leaf light saturation to occur at a PAR level of about 500 $\mu mol\,m^{-2}\,s^{-1}$ for *Cyrilla racemiflora* and *Clethra occidentalis* growing in the vicinity of the Mull forest plot (*Tanner* [1977a]; *cf.* Fig. 2.1). These two species make up 20 % and 6 % of the total basal area in both the MMor and the PMull forest plots, respectively (see Section 2.3.1). Based on the PAR/R_s relationship of Eq. 4.4, intensities of

R_s would have to exceed at least 250 Wm^{-2} to meet the threshold suggested by *Aylett* [1985] to be non-limiting to leaf productivity, at least in the upper canopy. On average, radiation levels at Bellevue Peak were above this limit for 52 % of all day-time hours and for 80 % of the time that light was potentially non-limiting (on average between 07:30 and 17:10 h). Applying the lower limit of 200 $\mu mol\, m^{-2}\, s^{-1}$, these values would increase to 77 % and 92 %. Even on fully clouded days, PAR levels were still above 200 $\mu mol\, m^{-2}\, s^{-1}$ for approximately 8 h, although maximum intensities did not exceed 400 $\mu mol\, m^{-2}\, s^{-1}$, *i.e.* 100 $\mu mol\, m^{-2}\, s^{-1}$ below the saturation limit suggested by *Aylett* [1985]. It can therefore be concluded that, despite the undeniable reduction in both solar- and photosynthetically active radiation under conditions with heavy cloud, the overall light climate in the study area is such that a consistent restriction of the photosynthetic apparatus is not to be expected. This, and the fact that the same overall light regime applies to both tall and stunted forest communities, eliminates persistently low radiation levels as a decisive factor determining forest stature in the study area.

The regression parameters found for the linear relationship between daily R_s and R_n (Eq. 4.3), *i.e.* 0.61 (slope) and 2.57 (y-intercept), are partly determined by the interaction between canopy structure and radiation exchange [*Brutsaert*, 1982]. The slope value corresponds closely with the 0.6 reported by *Turton* [1990] for a lower montane rain forest of taller stature in Queensland, northern Australia.

At 0.11 ± 0.01, the presently found value for the albedo is slightly lower than generally reported for (lowland) rain forest (0.12–0.14; *Oguntoyinbo* [1970]; *Pinker et al.* [1980]; *Culf et al.* [1995]) and bears more similarity to values derived for temperate- and tropical pine plantation forests (0.09–0.11; *Stewart* [1977]; *Waterloo et al.* [1999]). *Brünig* [1970] hypothesized that heath forests on white (infertile) sands, a tropical lowland vegetation type which shares a number of physiognomic characteristics with upper montane rain forest [*Whitmore*, 1998], may have a higher albedo compared to taller-statured rain forest in order to reduce its evapotranspiration and so minimize soil water deficiency. Similarly, *Medina et al.* [1978] suggested that the sub-vertical leaf orientation observed in heath forest and UMRF alike [*cf. Cavelier*, 1988] may serve to minimize the heat load of a canopy that is not cooled sufficiently because of restricted transpiration. However, contrary to Brünig's hypothesis, the presently found value for the albedo of a reasonably sclerophyllous montane rain forest, is slightly lower than that reported for most broad-leaved lowland forests.

4.5.2 Occurrence of fog and its contribution to overall precipitation inputs

Depending on cloud characteristics and persistence, vegetation structure, and wind speeds, amounts of cloud water (CW) intercepted by the vegetation may constitute a significant additional input of water in some tropical montane forests [*e.g. Weaver*, 1972; *Cavelier and Goldstein*, 1989; *Mamanteo and Veracion*, 1985; *Stadtmüller and Agudelo*, 1990] but do not always lead to noticeable

increases in net precipitation [*Steinhardt*, 1979; *Veneklaas and Van Ek*, 1990; *Cavelier et al.*, 1997; *Clark et al.*, 1998]. The perceived importance (or lack) of *CW* in the previous examples is mainly based on the relative magnitude of the throughfall component (*Tf*) compared to incident rainfall. A high *Tf*/*P* ratio suggests a substantial contribution by *CW* and *vice versa*. As shown by the present results (Section 4.4.2), the quantification of the amounts of *CW* actually intercepted by the forest canopy proved difficult. A comparison of amounts of net precipitation observed for conditions with and without fog did not generate statistically conclusive results (Table 4.3). Similar problems were encountered by *Schellekens et al.* [1998] in an 'elfin' cloud forest at 1015 *m* a.s.l. in Puerto Rico. They reported a value 6.6 % of *P* for *CW* during a short-term study whereas longer term *Tf* and *Sf* observations in the same forest by *Weaver* [1972] suggested net rainfall (*Tf*+*Sf*) to range between 99–106 % of *P* depending on site exposure, and contributions of *CW* of 0.09–0.15 *mm* moisture input per *mm P*. However, *Weaver* [1972] suggested that, particularly on the ridges, the additional input of water consisted of wind-driven (horizontal) rainfall rather than intercepted cloud moisture.

The presently adopted conservative estimates of 3.4 % and 1.4 % of *P* for *CW* in the MMor and PMull sites, respectively, probably rank at the low end of the recorded spectrum [*Bruijnzeel and Proctor*, 1995]. However, it should be realized that these estimates do not include any cloud water deposited during rainfall events themselves, nor during the first 2 *h* after rainfall (*cf.* section 4.3). As such, they must be considered underestimates. Although the presently adopted values are believed to be in the right order of magnitude [*cf. Weaver*, 1972; *Schellekens et al.*, 1998], further work is needed to substantiate these findings, also in terms of spatial variability (which was shown to be large).

Depending on gauge exposure, the extra contribution by cloud water ranged from 0.1 % (in the clearing at Bellevue Peak), via 12 % (above the MMor canopy) to 22 % (above the canopy at Bellevue Peak). Using a similar type of gauge, *Cavelier et al.* [1996] derived values of 2.5–149 % of *P* along an altitudinal transect in western Panama. They described the extra catch invariably to cloud water inputs, although a strong reduction in the amounts of ordinary rainfall at the most exposed sites would suggest wind-driven rain to be important as well. Increased wind speeds are known to reduce the catch efficiency of standard rain gauges [*e.g. Rodda*, 1967] while creating serious overestimation when fog gauges are used. As such, there is reason for caution when interpreting the results obtained with non-shielded 'Grünow' gauges on wet tropical mountains that are exposed to high wind [*cf. Schemenauer and Cereceda*, 1994; *Juvik and Nullet*, 1995]. Future studies could usefully employ recent advances in the modelling of *CW* deposition on the basis of topography, wind speed, vegetation, and cloud characteristics [*Bridgman et al.*, 1994; *Walmsley et al.*, 1999]. At any rate, the presently estimated amounts of *CW* must be considered too small to significantly affect forest ecological processes [*Bruijnzeel and Veneklaas*, 1998].

4.5.3 Reduced atmospheric evaporative demand

The low stature of some tropical montane forests has also been thought to be caused by extremely low, because climatically suppressed, rates of water and nutrient uptake [*Odum*, 1970; *Weaver et al.*, 1973; *Ash*, 1987]. Whilst this idea has already been shown to be erroneous on purely theoretical plant physiological grounds [*Grubb*, 1977], the present climatic observations do not support it either. Transpiration in tall LMRF usually amounts to 50–70 % of the open-water evaporation rate (E_0) according to *Penman* [1956], whereas values for smaller-statured forests are closer to 20–25 % [*Bruijnzeel et al.*, 1993; *Hafkenscheid*, 1994; *Holwerda*, 1997]. The mean E_0 of 3.0 $mm\,d^{-1}$ obtained by the present study, although somewhat lower than the 4.5–5.0 $mm\,d^{-1}$ typically found in lowland conditions [*Bruijnzeel et al.*, 1993], must be considered quite high in view of the fact that it was obtained for an elevation of 1849 m. Rather, the present value falls in the 2–4 $mm\,d^{-1}$ range that is normally reported for low to intermediate elevations (<1000 m) [*Bruijnzeel et al.*, 1993; *Holwerda*, 1997]. More importantly, even at 20–25 % of E_0, the values of E_0 in the study area would be more than sufficient to enable an adequate uptake of water, thereby invalidating the assumption that the atmospheric demands on wet tropical mountains would limit the possibility for nutrient uptake. The consequences of the high precipitation excess over forest evaporation at the study sites are examined in Chapter 5. It is concluded that neither excessive waterlogging nor regular soil water stress were important determinants of forest stature.

4.6 Conclusions

In conclusion, our meteorological observations provide no direct evidence for significantly lowered plant production potential in the study area, be it through reduced leaf temperatures, radiation or atmospheric evaporative demands, besides the fact that such restrictions, if existing at all, would apply to both tall-statured and stunted forest communities alike. Furthermore, neither excessive soil wetness, high cloud water incidence and prolonged canopy wetness, nor severe droughts are important in the study area.

It is concluded therefore that unfavourable (non-physical) edaphic conditions (such as high acidity, excess aluminium and low key nutrients) must be held responsible for the observed low effective net above-ground productivity in the more stunted forest types in the study area [*Tanner*, 1980a, 1985] which, in turn, may express itself as a retardation in growth.

5

WATER BUDGETS OF TWO UPPER MONTANE RAIN FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA*

ABSTRACT

The water budgets of a relatively tall (7–12 m, PMull) and a stunted tropical montane forest (5–8 m, MMor) spaced <30 m apart at c. *1820 m in the Blue Mountains, Jamaica, were determined over 1995 using complementary hydrological and micrometeorological techniques. Rainfall amounted to 3060 mm yr^{-1}, cloud water interception was estimated at 1.4 and 3.4 % of incident rainfall in the tall and the stunted forest, respectively. Net precipitation (throughfall+stemflow) amounted to 86 and 78 % of gross precipitation (2630 and 2380 mm), giving a rainfall interception (E_i) of 430 and 680 mm (14 and 22 % of annual P), respectively. At 13 and 18 % of rainfall, the stemflow fractions in both the tall and the stunted forest were exceptionally high. Transpiration (E_t) was calculated using the Penman-Monteith equation and meteorological observations above low regenerating forest vegetation at nearby (<150 m) Bellevue Peak (1849 m a.s.l.). Average E_t for the 233 days for which a complete meteorological record was available was 1.52 mm d^{-1} (maximum 4.4 mm d^{-1}). Over 1995, E_t was estimated at 1.39 mm d^{-1} or 509 mm yr^{-1} (16.6 % of P) for the vegetation at Bellevue Peak and for the stunted MMor forest. For the taller-statured PMull forest E_t was estimated at 1.7 mm d^{-1} or 620 mm yr^{-1} (20.3 % of P). Adding E_i and E_t gave about 1050 and 1190 mm yr^{-1} for total forest evaporation (ET) in the taller and the stunted forest, respectively.*

Drainage was computed with a one-dimensional SVAT *model (*VAMPS*) and equalled 2032 mm yr^{-1} in the taller forest vs. 1857 mm yr^{-1} in the stunted forest. Corresponding changes in soil moisture storage were small (−20 and +14 mm). Modelling the influence of drought on forest stature indicated that dry periods would have to exceed c. 40 and 14 days to generate possible water stress (soil moisture tensions ≤−100 kPa) in the taller and the stunted forest, respectively, whereas c. 18 and 6–12 dry weeks (depending on the horizon) would be required to reach permanent wilting point (soil moisture tensions ≤−1.58 MPa).*

*With L. A. Bruijnzeel, R. A. M. de Jeu and N. J. Bink. A summary of this chapter was presented at the Second International Colloquium on Hydrology and Water Management in the Humid Tropics, March 22–26, 1999, Panama City.

In conclusion: (i) Differences in net precipitation inputs between the two sites are insufficient to explain the contrasts in stature and physiognomy between the taller and the stunted forest; (ii) The estimated transpiration rates are comparable to those reported for tall montane forests that experience little to no cloud; this is supported further by the small amounts of cloud water intercepted by the two forests; (iii) The stunted forest appears to be slightly more sensitive to drought than the taller forest but the long dry periods required to cause significant soil water stress are unlikely to happen under the prevailing rainfall regime.

5.1 INTRODUCTION

Tropical montane forests are under increasing anthropogenic pressure [*Doumenge et al.*, 1995] and fears have been expressed that the loss of headwater forests subject to frequent cloud incidence (so-called tropical montane cloud forests (TMCF); *Stadtmüller* [1987]) may adversely affect the water supply to densely populated lowlands, particularly during rainless periods [*Zadroga*, 1981; *Stadtmüller*, 1987; *Brown et al.*, 1996]. However, although TMCFs are known to receive additional inputs of water via intercepted cloud water, these amounts of 'horizontal precipitation' are extremely variable, both in time and space [*Bruijnzeel and Proctor*, 1995; *Brown et al.*, 1996; *Bruijnzeel*, 1999]. Similarly, whilst water use by TMCF is allegedly low, reliable information on the subject is extremely scarce. Estimates of transpiration E_t are mostly based on catchment water budgets in which forest water uptake is evaluated by subtracting amounts of rainfall interception from total evapotranspiration (ET) [*Bruijnzeel and Proctor*, 1995].

Also, montane cloud forests may show considerable differences in stature, ranging from tall (up to 30 m; *Steinhardt* [1979]) to stunted (down to 2–3 m; *Howard* [1968]). A host of hypotheses have been advanced to explain such differences in stature and many of these involve a hydrological element. Persistent waterlogging, occasional drought on shallow soils, climatically reduced water uptake, and severe leaching of the substrate have all been suggested as a potential cause of forest stunting on wet tropical mountains [*Bruijnzeel and Proctor*, 1995].

Within the framework of a comparative study of the causes of forest stunting the components of the water budgets of two nearly adjacent upper montane rain forests of contrasting stature in the Blue Mountains of Jamaica were studied between 1 January 1995 and April 1996. The shorter-statured forest (main canopy height 5–8 m) of the two was situated at 1824 m a.s.l. on an exposed ridge top and was classified as a 'moderately-developed' Mor forest. The taller-statured forest (7–12 m) was located 30 m away on an almost level section of the NW slope of the same ridge at an elevation of 1809 m a.s.l. and was classified as a 'poorly-developed' Mull forest (PMull). The adjectives 'poorly-' and 'moderately-developed' refer to the relative position of the sites within a sequence of montane forest types previously recognized by *Grubb and Tanner*

[1976] and *Tanner* [1977a] (see Chapter 2 for argumentation).

The present paper reports on the water budgets of the two forests over the year 1995 as a preliminary to a discussion of water-borne nutrient fluxes (Chapter 7). A detailed discussion of the climatic conditions in 1995 as measured at 1849 m a.s.l. on nearby (<150 m) Bellevue Peak (see Fig. 2.1 in Chapter 2) has been given in Chapter 4.

5.2 Study area

A detailed description of the structural, floristic and soil characteristics of the two study forests (PMull and MMor) has been given in Chapter 2. Summarizing, the PMull forest plot (area 300 m^2) has a main canopy height of 7–12 m and an estimated LAI of 5.0 m^2m^{-2} (Section 4.4.3). Tree density of this forest type is 4400 trees per ha of which 570 trees per ha have multiple trunks. For the MMor forest (area 240 m^2) the corresponding values are 5–8 m, 4.1 m^2m^{-2}, 6040 trees ha^{-1}, and 1040 trees ha^{-1} with multiple trunks, respectively (Table 2.1). Despite these structural differences, the two forests exhibit a large overlap in species (Table 2.2).

The soils of the MMor forest (Folic histosol) and the PMull forest (Dystric cambisol) differ markedly (see Fig. 2.6 and Appendix A for details). In the PMull, a discontinuous ectorganic horizon (<4 cm) overlies a leached clayey mineral soil, with increasing amounts of weathered andesitic parent material with depth and the mass of fine roots gradually decreasing with depth. Topsoil porosity (*c.* 80 % in the Ah horizon) decreases to *c.* 60 % in the subsoil. Median values (means given in Table 5.1) of saturated hydraulic conductivity (K_{sat}) range from 10.1 $m\,d^{-1}$ in the Ah-horizon to <1 $cm\,d^{-1}$ in the Bw2 horizon.

The soil in the MMor is characterized by a thick high-surface root mat and accumulation of slowly decomposing acid mor humus (thickness ≤50 cm) above a shallow soil profile (≃70 cm). The MMor soil is also highly leached but more acid (pH_{CaCl_2}<4.0) and less clayey than the PMull soil, with andesitic parent material occurring in the subsoil. Porosity of the MMor subsoil is slightly higher than in the PMull. K_{sat} decreases again with depth. Median values for K_{sat} range from *c.* 18.5 $m\,d^{-1}$ in the Ah–Bh to *c.* 1 $m\,d^{-1}$ in the BC horizon.

5.3 Methodology

General

For a vegetated surface subject to mist or low cloud, the equation for the water balance over a given period of time reads:

$$P + CW = E_i + E_t + E_s + R + D + \Delta S \tag{5.1}$$

where P is incident rainfall, CW cloud water interception, R surface runoff (overland flow), D drainage, and ΔS the change in soil moisture storage. The evaporation terms E_i, E_t, and E_s represent the losses via intercepted precipitation (evaporation from a wet canopy), transpiration (evaporation from a dry

Table 5.1: Variations with depth of soil texture (clay<$2\mu m$≤silt≤$63\mu m$-<sand≤$2mm$<gravel, %), bulk density (BD, $g\,cm^{-3}$), saturated hydraulic conductivity (K_{sat}, $m\,d^{-1}$), porosity (%), volumetric water content (θ, $cm^3\,cm^{-3}$) at water tensions of -10 *kPa* ($pF = 2$: 'field capacity'), -100 *kPa* ($pF = 3$), and -1.58 *MPa* ($pF = 4.2$: 'permanent wilting point') and amounts of plant available water (PAW, $\theta_{pF2} - \theta_{pF4.2}$, $cm^3\,cm^{-3}$) at the PMull and MMor forest sites*.

Forest	Horizon	Depth	clay	silt	sand	gravel	BD	K_{sat}	Porosity
		[cm]		[%]			[$g\,cm^{-3}$]	[$m\,d^{-1}$]	[$cm^3\,cm^{-3}$]
PMull	Ah	0–14	28.7	40.3	31.0	0.0	0.44	13.8	0.79
	Bh	14–38	22.6	21.9	53.8	1.7	0.84	0.23	0.68
	Bw1	38–65	7.3	6.7	46.0	40.0	0.98	0.24	0.64
	Bw2	65–82	18.6	20.2	49.1	12.1	1.07	0.01	0.61
			θ_{pF2}	θ_{pF3}	$\theta_{pF4.2}$	PAW			
	Ah	0–14	0.455	0.227	0.099	0.356			
	Bh	14–38	0.523	0.336	0.190	0.333			
	Bw1	38–65	0.512	0.310	0.160	0.352			
	Bw2	65–82	0.552	0.362	0.180	0.372			
MMor	Ah	0–5	21.4	24.0	51.3	3.3	0.39	89.9	0.78
	Bh	5–10	6.4	6.0	36.2	44.4	0.54	23.4	0.78
	Bw	10–35	4.1	3.0	48.4	44.5	0.61	13.7	0.75
	BC	35–≃70	5.2	4.1	51.2	39.5	0.81	1.4	0.63
			θ_{pF2}	θ_{pF3}	$\theta_{pF4.2}$	PAW			
	Ah	0–5	0.369	0.210	0.109	0.260			
	Bh	5–10	0.399	0.206	0.094	0.305			
	Bw	10–35	0.358	0.190	0.090	0.268			
	BC	35–≃70	0.411	0.204	0.087	0.324			

*See Chapter 2 for details on methodology.

canopy) and evaporation from the soil and litter complex, respectively. Their sum equals total evapotranspiration (ET). All components of the water budget are expressed in mm of water for the chosen time interval.

E_s is generally very small in tropical rain forests [*Jordan and Heuveldop*, 1981; *Roche*, 1982] and can be neglected therefore. Here E_s is included in the estimate of E_t (see below). Surface runoff was never observed (which is expected given the high permeability of the soils; Table 5.1). As such, Eq. 5.1 reduces to:

$$P + CW = E_i + E_t + D + \Delta S \tag{5.2}$$

The different forest types of the study area occur in small patches along and around narrow ridge tops (*Grubb and Tanner* [1976]; Chapter 2). This precluded the use of the catchment water balance approach in which streamflow (equalling $R + D$ in Eq. 5.1) is monitored and ET evaluated by subtracting streamflow from $P + CW$ [*Ward and Robinson*, 1990]. Although Eq. 5.1 can be solved in principle on a plot basis as well, the estimation of the drainage component is notoriously difficult because of the large spatial variability of the hydraulic conductivity of forest soils [*Cooper*, 1979; *Davis et al.*, 1996]. Therefore, use is often made of alternative techniques to determine E_t, such as micro-meteorological [*cf. Shuttleworth*, 1988] or plant physiological methods [*Roberts et al.*, 1999]. The mosaical character of the vegetation in the study area precluded the application of micro-meteorological techniques to evaluate E_t separately per forest type because the fetch requirements of such techniques could not be met [*Thom*, 1975]. Therefore, a combination of hydrometeorological and plant physiological methods was envisaged initially for the determination of E_i and E_t, respectively, per plot.

Unfortunately, the Greenspan sapflow gauges that were used on a series of nine sample trees of variable diameters in each plot could not cope with the humidity of the prevailing climate and failed to give any useful results. Therefore, an alternative strategy had to be followed. Along with the continuous measurement of basic climatic variables (temperature, humidity, global and net radiation, wind speed and direction) above the freely exposed short (*c.* 3 *m*) regenerating forest vegetation of similar floristic composition on Bellevue Peak (1849 *m* a.s.l.; lateral distance to the two forest plots <150 *m* towards the NE), a set of thin-wire thermocouples was used to measure rapid fluctuations in temperature. From the latter, an estimate of E_t can be derived [*Vugts et al.*, 1993; *Waterloo et al.*, 1999]. It was recognized from the outset that there would be differences in aerodynamic roughness and, especially, surface resistance between the vegetation at Bellevue Peak and each of the two study plots. As such, the estimates of E_t presented in the following for the regenerating forest at Bellevue Peak must be considered a first approximation of the water uptake of the mature forests of the plots. In the following the methodology used to quantify E_i, E_t, D and ΔS will be described whereas details of the instrumentation are given in Section 5.4.

Interception loss

Rainfall interception (E_i) was evaluated as the difference between incident

rainfall and the sum of throughfall (Tf) and stemflow (Sf). Because the latter was measured on a 3–4 day basis (see Section 5.4 for details), the analytical model of rainfall interception developed by *Gash* [1979] and modified later by *Gash et al.* [1995] was used to generate a daily record of both Tf and Sf of the forest structural parameters required by the analytical model. the canopy saturation value S, stemflow coefficient p_t and trunk capacity S_t were derived using the methods of *Jackson* [1975] and *Gash and Morton* [1978], respectively. The free throughfall coefficient p, *i.e.* the gap fraction of the forest canopy, was derived using ceptometer measurements of photosynthetic active radiation above and below the respective canopies (see Section 4.3 for details).

Transpiration
Daily values of E_t were evaluated using the Penman-Monteith equation [*Monteith*, 1965]:

$$\lambda E = \frac{\Delta A + \rho C_p VPD/r_a}{\Delta + \gamma(1 + r_s/r_a)} \tag{5.3}$$

where:

λE	latent heat flux	$[W m^{-2}]$
A	available energy	$[W m^{-2}]$
Δ	slope of the saturation vapour pressure curve at air temperature T	$[Pa\,K^{-1}]$
γ	psychrometric constant	$[Pa\,K^{-1}]$
C_p	specific heat of air	$[J\,kg^{-1}K^{-1}]$
ρ	density of air	$[kg\,m^{-2}]$
VPD	vapour pressure deficit	$[Pa]$
r_a	aerodynamic resistance	$[s\,m^{-1}]$
r_s	surface resistance	$[s\,m^{-1}]$

For wet canopy conditions the surface resistance r_s reduces to zero, which allows Eq. 5.3 to be simplified to:

$$\lambda E = \frac{\Delta A + \rho C_p VPD/r_a}{\Delta + \gamma} \tag{5.4}$$

The aerodynamic resistance r_a was calculated from wind speed observations above the regenerating forest at Bellevue Peak assuming a logarithmic wind profile and neutral stability conditions according to [*Thom*, 1975]:

$$r_a = \frac{(ln\left[\frac{z-d}{z_0}\right])^2}{k^2 \cdot u} \tag{5.5}$$

where:

z	observation height above the ground surface	$[m]$
d	zero-plane displacement height	$[m]$
z_0	roughness length	$[m]$
k	von Kármán's constant, 0.41	[-]
u	wind speed as measured at height z	$[m\,s^{-1}]$

Considering the short stature of the vegetation at Bellevue Peak and the dissected nature of the terrain in general, d was set at 0.6 times the canopy height h (3.0 m) or 1.8 m [*cf. Monteith and Unsworth*, 1990]. Wind profile data used in the analysis were restricted to wind speeds in excess of 3 $m\,s^{-1}$ at the lowest level (5.9 m) and to wind directions between 40° and 160° to avoid non-neutral atmospheric conditions and fetch limitations. Finally, wind speeds as measured at 5.9 m were converted to those expected at 3.5 m level (where most other climate parameters were measured) using a logarithmic wind profile [*Thom*, 1975].

Values of $z_0 + d$ were derived for 3742 half-hourly periods with (near) neutral atmospheric stability and adequate fetch using the graphical method proposed by *Thom* [1975]. An average value of 2.25 m was obtained, giving a value of z_0 of 0.45 m (0.15 × the vegetation height at Bellevue Peak). Converting wind speeds measured at 5.9 m to those predicted by the logarithmic wind profile for 3.5 m reduces Eq. 5.5 to:

$$r_a = \frac{10.51}{u_{3.5m}} \tag{5.6}$$

The resistance parameter r_s was evaluated by an inverse application of the Penman-Monteith equation, a method that requires independent estimates of λE [*Monteith*, 1965]. These were obtained by solving a simplified energy budget equation. Assuming that (i) amounts of advected energy and various small physical and biochemical storage terms are small (and therefore negligible); and (ii) the resulting available energy ($R_n - G$) is used either for warming up the ambient air or for evapotranspiration [*Brutsaert*, 1982] we can write:

$$R_n - G = H + \lambda E \tag{5.7}$$

where:

R_n	net radiation flux density	$[Wm^{-2}]$
G	soil heat flux density	$[Wm^{-2}]$
H	sensible heat flux density	$[Wm^{-2}]$
λE	latent heat flux of vaporization	$[Wm^{-2}]$
λ	latent heat of vaporization	$[J\,kg^{-1}]$

R_n and G were measured directly (Section 5.4) as part of the meteorological observations at Bellevue Peak. The sensible heat flux H was obtained using the temperature variance method [*Tillman*, 1972; *De Bruin*, 1982]. Under dry unstable atmospheric conditions, H is related to near-surface turbulent fluctuations in air temperature, the intensity of which is described by the standard deviations (σ_T) of high-frequency measurements of the air temperature T (K). The underlying theory of the method is summarized ed in Appendix B.

As this procedure is restricted to periods during which the forest canopy is dry, λE refers to transpiration E_t as well as to evaporation from the litter surface E_s. Next, the values for $\lambda E = E_t + Es$ obtained with the temperature variance method were employed in an inverse application of the Penman-Monteith equation and inserting measured climatic conditions:

$$r_s = \frac{\rho C_p}{\gamma}\frac{VPD}{\lambda E} + r_a\left(\frac{\Delta(R_n - G)}{\gamma \lambda E} - \frac{\Delta}{\gamma} - 1\right) \tag{5.8}$$

The resulting half-hourly values of r_s were subjected to a multiple-regression analysis and related to corresponding ambient climatic variables to permit solving of the Penman-Monteith equation during periods for which thermo-couple data were not available [*cf. Waterloo et al.*, 1999].

Drainage and soil moisture storage
Because soil water tension profiles were only measured at 3–4 day intervals, the one-dimensional Soil-Vegetation-Atmosphere-Transfer (SVAT) model VAMPS [*Schellekens*, 1996] was used for the computation of daily values of D and ΔS. A summary description of the VAMPS model is given in Appendix C.

Soil moisture retention curves (ψ_m – θ relationships) needed to solve the basic equation for unsaturated flow [*Richards*, 1931] as used in the SVAT model VAMPS (Appendix C) were derived using undisturbed soil cores (100 cm^3; typically 5–8 per horizon). The ψ_m – θ relationships were established using the porous medium *cum* pressure-membrane technique [*Black et al.*, 1965; *Stakman*, 1973]. Saturated hydraulic conductivities (K_{sat}) were measured with an ICW permeameter, using falling- and constant-head approaches for samples of low and high permeability, respectively [*Kessler and Oosterbaan*, 1973]. Unsaturated conductivity $K(\theta)$ was derived from measured saturated conductivity and the relations between soil water content, suction head and $K(\theta)$ using the so-called Van Genuchten equations [*Van Genuchten*, 1980] (see Appendix C for details).

The upper 80 *cm* of the mineral soil profiles of the PMull and MMor forest plots were subdivided into 80 sub-layers of 1 *cm* each to enable the adequate simulation of the rapid fluctuations in top soil water tension ψ_m that are known to occur in the study area [*Kapos and Tanner*, 1985]. Active rooting depths of 60 and 30 *cm* were assigned to the PMull and MMor soils, respectively [*Elbers*, 1996]. Free drainage at the profile bottom was assumed in this study. The net precipitation record generated with the analytical model of rainfall interception and the estimates of E_t as computed with Eq. 5.3 were taken to represent the amounts of water added to or extracted from the soil water reserve on a daily time step. Water uptake by the roots would start to deviate linearly from the potential rate indicated by Eq. 5.3 whenever $\psi_m \leq -100$ *kPa* ('limiting point', $pF = 3$; *Landsberg* [1986]) whereas transpiration stopped entirely at $\psi_m \leq -1.58$ *MPa* ('permanent wilting point', $pF = 4.2$). An initial profile for ψ_m with depth was generated by interpolating the values measured at four depths on 1 January 1995 over the 80 sub-layers.

The ψ_m values predicted by the VAMPS model were calibrated against values measured by 3–4 tensiometers in each of the four principal soil horizons during the 208 day record for which continuous estimates of E_t were available (1 January – 27 July 1995). To obtain optimum agreement between predicted (mean values for 5 sub-layers of 1 *cm* each around a soil horizon's centre) and measured values of ψ_m, the magnitude of the saturated hydraulic conductivity (K_{sat}) was adjusted. The optimizations were restricted to a single parameter only for reasons of transparency and because values of K_{sat} in forest soils can be grossly underestimated when using small cores [*Davis et al.*, 1996].

5.4 INSTRUMENTATION

Rainfall (P, mm) at Bellevue Peak was measured above the vegetation at 3.5 m with a tipping bucket cum logger system (resolution 0.44 mm) manufactured at the Vrije Universiteit Amsterdam, backed by two manual gauges (100 cm^2 orifice) placed in a nearby clearing. The auto-recorded data were stored at 5-min intervals whereas the manual gauges were read every 3–4 days. From 21 July 1995 onwards, a manual rain gauge was also operated above the canopy of the MMor forest and read at 3–4 day intervals.

Amounts of *cloud water* intercepted by a forest are bound to differ from those estimated with a simple standard fog gauge [*Schemenauer and Cereceda*, 1994; *Hafkenscheid et al.*, 1998]. Therefore, although Grünow-type fog gauges [*Russell*, 1984] were installed above the vegetation at Bellevue Peak and the MMor forest, cloud water intercepted by the two forest plots was estimated as all throughfall that did not originate from rainfall. The underlying assumption is that all Tf recorded after the last registration of P had to be generated by CW after applying a threshold of 2 h to eliminate contributions by residual rainfall-induced crown drip [*cf. Schellekens et al.*, 1998]. It is recognized that amounts of CW obtained in this way will represent minimum estimates.

Throughfall (Tf) was measured in the MMor and PMull forests with tilted (30°) stainless steel gutters (400 × 4 cm) equipped with a tipping bucket cum logger device (0.3 mm per tip) in combination with twelve manual gauges (100 cm^2 orifice; 3–4 day sampling intervals) which were randomly relocated after each sampling [*Lloyd and Marques-Filho*, 1988]. An areal average Tf volume was obtained by a weighting procedure that took the relative areas of the two types of gauges into account. The gutters were cleaned every 3–4 days and regularly treated with a teflon solution to prevent blockage by organic debris and to minimize wetting losses, respectively. In each plot, twelve trees, representing a range in species and diameter classes, were fitted with rubber collars connected to 22.5 litre containers to measure *stemflow* (Sf). Gauges were emptied simultaneously with those for Tf while dividing the Sf volumes by the projected area of the corresponding tree crowns enabled their expression in mm of water.

The meteorological mast at Bellevue Peak was in operation from 1 January 1995 until 4 April 1996, with the exception of 28 July–21 October 1995, 16 November–15 December 1995 and 30 December 1995–16 January 1996 when parts of the equipment were damaged by excessive moisture (1996) or lightning strikes (1995). To improve the seasonal representativity of the data, the present chapter is restricted to the observations made in 1995.

Net radiation (R_n, Wm^{-2}) was measured with a net radiometer (Radiation and Energy Balance Systems Inc.) placed at 5.9 m on an arm extending 1.5 m from the mast in such a way as to avoid shading of the instruments. Net soil heat fluxes (G_s, Wm^{-2}) were determined with a soil heat flux plate (Middleton & Co.) placed underneath a *c.* 5 cm thick litter layer. Care was taken to avoid disturbance of the litter layer during installation. Air temperature (T,

^{o}C) and relative humidity (RH, percentage of saturation) were measured at 3.5 m with a precision thermometer (Campbell Sci. HMP 35AC) and Vaisala capacitative humidity sensor after 60 s of forced ventilation at approximately 2 $m\,s^{-1}$. Both sensors were placed in a Gill-type radiation shield to protect them against direct insolation and rainfall. The thermometer had an accuracy of 0.1 ^{o}C. The accuracy of the RH sensor was typically better than 2 % whereas a long-term stable precision of less than 1 % was stated by the manufacturer. Relative humidity readings in excess of 100 %, as were recorded sometimes during periods of prolonged wetness, were set at 100 %. Both T and RH sensors were calibrated regularly against readings made with an Assmann psychrometer. Wind direction was measured using a potentiometer windvane (Vector Instruments, W200P) placed at 12.5 m. Wind speeds were determined at three heights (5.94, 7.65, and 10.1 m) using three-cup anemometers (Vector Instruments, A101M/L), supported by arms (0.5 m) orientated towards the prevalent wind direction (ESE). The sensors had a stalling speed of 0.15 $m\,s^{-1}$ and an accuracy of 1–2 %. All instruments were sampled at 30-s intervals except for the T and RH probes (every 5 min). A fast-responding dry-bulb thermo-couple (chromel-constantane wire type; 12.7 μm wire thickness; *Tillman* [1972]) was used for the registration (0.5 Hz) of rapid fluctuations in air temperature at 5.9 m (2.9 m above the forest canopy) to derive the sensible heat flux H (see Appendix B for details). Thermocouple data were pre-processed over 5-min intervals to avoid trends in standard deviation values. All data were processed by a Campbell 21X data logger system. Averages and standard deviations were calculated over 30-min periods and stored using a solid state memory.

Soil water tensions ψ_m were determined at three sites within each forest, with a total of 14 tensiometers per plot distributed over the principal soil horizons (8 in the top horizons, 6 in the subsoil horizons) and read at 3–4 day intervals (*i.e.* the same as for the measurements of throughfall and stemflow). A needle cum pressure transducer system was used that was accurate to the nearest centimeter, up to tension values of *c.* -0.9 MPa ($pF = 2.9$; air entry value).

5.5 Results

5.5.1 Rainfall and cloud water deposition

Rainfall input over the year 1995 at Bellevue Peak amounted to 3060 mm, *i.e.* about 7 % above the estimated average annual rainfall for the research area (2850 mm; Chapter 2) and *c.* 25 % above the long-term mean annual rainfall record for nearby Cinchona (2277 $mm\,yr^{-1}$; 1901 – 1990; J. R. Healey, *personal communication*). Amounts observed at Bellevue Peak and above the MMor forest did not differ significantly and the latter will not be considered further. Rainfall was also unevenly distributed over the year: October and November were even wetter than normal (>450 mm each) whereas the secondary peak that normally occurs in May and June was absent. The generally rather dry February– March period, on the other hand, was distinctly wetter than usual

Fig. 4.1). Over 1995, the automated equipment identified 327 separate events distributed over 205 days with rain in excess of 0.44 *mm*, with an average of 14.9 *mm* per rain day. A total of 71 dry periods of 24 hours or more were recorded (mean duration: 2.3 days; 160 days in total) of which 51 (72 %) were of less than 48 hours duration. The longest continuously dry period lasted 11 days (27 March to 6 April). Average values for storm size, duration and intensity were 9.41 *mm*, 02:13 *h*, and 5.12 $mm\,h^{-1}$ (weighted mean 4.2 $mm\,h^{-1}$), respectively. The highly skewed frequency distributions of these parameters however requires the use of median rather than mean values: 1.78 *mm*, 0:40 *h*, and 2.36 $mm\,h^{-1}$ (see Section 4.4.1 for a more detailed description of rainfall characteristics).

Net cloud water deposition (*CW*) at the MMor plot in the form of *Tf* during rain-free periods totalled 93 *mm*. This amount equalled 3.4 % of the rainfall associated with the preceding storms. For the PMull plot the corresponding values read 31 *mm* and 1.4 % of *P*, respectively. Extrapolating these percentages to a one-year period, gives amounts of 43 $mm\,yr^{-1}$ for the taller but less exposed PMull forest and 104 $mm\,yr^{-1}$ for the shorter-statured but more exposed MMor. Both estimates must be considered conservative because an unknown amount of fog is intercepted by the forest during rainfall.

5.5.2 Throughfall, stemflow and derived estimates of rainfall interception

Total throughfall (*Tf*) amounted to 2233 *mm* in the taller-statured PMull forest and was 1821 *mm* in the stunted MMor forest. These values correspond to *c.* 73 % and 60 % of the associated rainfall. The corresponding *stemflow* (*Sf*) amounts were 399 and 559 $mm\,yr^{-1}$, respectively, or 12 % and 18 % of *P*. Automatically recorded *Tf* data were available for 257 and 307 days in the PMull and MMor forest, respectively. The correlation between the continuously recorded and the spatially averaged manual *Tf* data (3–4 day periods) was modest ($r^2 \leq 0.75$), largely as a result of high spatial variability in *Tf*, presumably because of frequently occurring drip points [*cf. Lloyd and Marques-Filho*, 1988].

Measured interception losses (E_i) amounted to 428 *mm* (14.0 % of *P*) in the PMull *vs.* 680 *mm* (22.2 % of *P*) in the MMor forest. The high interception estimated for the stunted MMor forest is surprising and largely due to its low *Tf* fraction because the *Sf* fraction is very high.

Table 5.2 lists the values of the four forest structural parameters (*p*, *S*, p_t, and S_t) that were used in the analytical model of rainfall interception, along with the average and median rainfall intensities and the rate of evaporation from a wet canopy (as computed with Eq. 5.4). The larger stature and LAI of the PMull forest are reflected in the higher values of the canopy and trunk storage capacities whereas the MMor forest has a higher gap fraction (*p*) and a higher stemflow coefficient (p_t). Fig. 5.1 shows the measured amounts and optimized model predictions of net precipitation (*Tf*+*Sf*) over 1995 for the PMull and MMor forests. Using the average value of 0.15 $mm\,h^{-1}$ for $\overline{E}_{wet}$ as calculated with Eq. 5.4 in the analytical model overestimated the measured E_i by 52 *mm* (1.7 % of *P*) in the PMull forest but gave an underestimation of 247 *mm* (−8.1

Table 5.2: Forest structural and climatic parameters used in an application of the analytical rainfall interception model for the MMor and PMull forests: the mean ($\overline{R}_i$) and median intensities of precipitation, the mean evaporation rate from a saturated canopy ($\overline{E}_{wet}$), the storage capacities of the canopy (S) and trunks (S_t), the coefficients of free throughfall (p) and stemflow (p_t), and the amounts of P necessary to saturate the canopy (P_s).

Forest	$\overline{R}_i$	R^{median}	$\overline{E}_{wet}{}^*$	p	S	p_t	S_t	P_s
	$mm\,h^{-1}$				-	mm	-	mm
PMull	5.12	2.36	0.154	0.05	1.57	0.15	0.39	2.0
MMor	5.12	2.36	0.154	0.13	1.30	0.20	0.20	2.2

*Computed with Eq. 5.4.

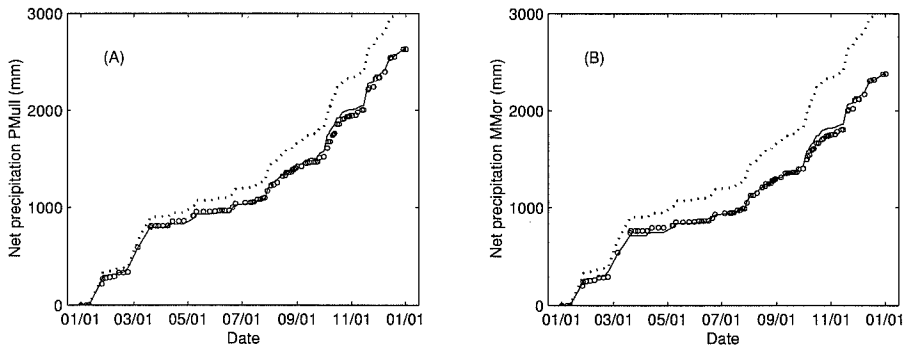

Figure 5.1: Observed (circles) and modelled (solid line) cumulative totals of net precipitation ($Tf+Sf$) over 365 days comprising 94 periods of manual sampling in the PMull (A) and MMor (B) forest, respectively. Gross precipitation (dotted line) has been added for comparison.

% of P) in the MMor forest. Optimizing the value of E_{wet} to match measured and modelled net precipitation totals gave a value of 0.11 $mm\,h^{-1}$ for the PMull forest (*i.e.* 40 % lower than the previous estimate of 0.15 $mm\,h^{-1}$) but required a 230 % increase to 0.36 $mm\,h^{-1}$ for the MMor forest. We will return to this discrepancy in Section 5.6.1.

5.5.3 Transpiration

Calculations of E_t using the Penman–Monteith equation (Eq. 5.3) require knowledge of the diurnal patterns of the aerodynamic (r_a) and surface resistance (r_s) parameters. The average diurnal pattern of r_a at Bellevue Peak (based on 253 days of wind speed observations) mirrors the pattern of lower wind speeds during the day and maximum wind speeds at night (*cf.* Section 4.4.3). Values for r_a increase during the day to a mid-afternoon maximum of *c.* 39 $\pm$ 22 $s\,m^{-1}$, followed by a rapid decrease in the late afternoon to a minimum and rather constant nocturnal value of 19 $\pm$ 15 $s\,m^{-1}$ (Fig. 5.2).

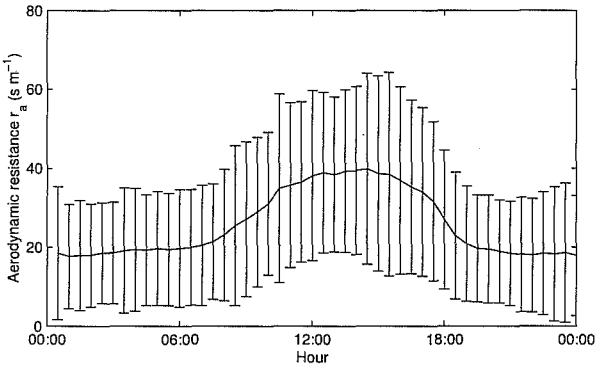

Figure 5.2: Average diurnal pattern of the aerodynamic resistance r_a for the vegetation on Bellevue Peak based on 253 days of wind speed observations between 1 January and 31 December 1995. Vertical bars represent ± one standard deviation.

Inverse application of the Penman-Monteith equation to derive values of r_s (Eq. 5.8) requires independent observations of the latent heat flux (evapotranspiration) λE. Using the temperature variance method (Equations B.1–B.5 in Appendix B) in combination with the energy budget (Eq. 5.7), λE of the regenerating forest at Bellevue Peak was derived for 411 half-hourly periods with dry canopy conditions and $R_n > 100\ Wm^{-2}$. The corresponding totals of net radiation (R_n), soil heat flux (G), and sensible heat flux (H) amounted to 264.7, 3.6 and 128.5 $MJ\,m^{-2}$, respectively, giving a total λE of 132.6 $MJ\,m^{-2}$ (equivalent to 54.0 mm of water given a mean value for λ of 2.46 $MJ\,kg^{-1}$). The average hourly rate of λE was 0.26 ± 0.16 $mm\,h^{-1}$ (maximum 0.72 $mm\,h^{-1}$). The average diurnal pattern of r_s derived from these 411 half-hourly values of λE by solving Eq. 5.8 is shown in Fig. 5.3. Values of r_s are lowest in the early morning (09:00 AM) and seem to increase steadily during the remainder of the day to reach values $\geq$100 $s\,m^{-1}$ in the night (Fig. 5.3).

To enable the extension of the above values of r_s to periods for which no thermocouple data were available, they were subjected to a multiple-regression analysis with ambient climatic variables, notably net radiation (R_n, Wm^{-2}), vapour pressure deficit (VPD, kPa), temperature (T, K) and wind speed at 3.5 m ($u_{3.5m}$, $m\,s^{-1}$) [*cf. Waterloo et al.*, 1999]. The resulting empirical relationship ($n = 411$, $r^2 = 0.67$) reads:

$$r_s = e^{-5.8525 - 0.0038 \cdot R_n - 0.0179 \cdot VPD + 0.6348 \cdot T - 0.1975 \cdot u_{3.5m}} \tag{5.9}$$

Eq. 5.9 was applied to all 3587 half-hourly records during which the canopy could be assumed to be dry and R_n >100 Wm^{-2}. During much of the day the resulting average pattern for r_s (shown in Fig. 5.3B) corresponds reasonably well with that derived using Eq. 5.8 (Fig. 5.3A) but large deviations occur in the early morning and in the late afternoon, when the TVAR-based estimates of r_s are higher. However, the associated standard deviations are so large that

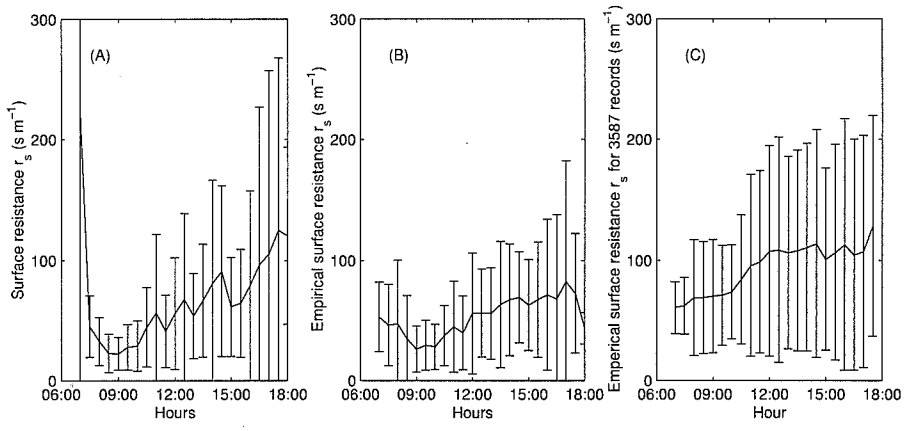

Figure 5.3: Average diurnal patterns of the surface resistance r_s for the regenerating vegetation at Bellevue Peak based on (A) solving Eq. 5.8 for 411 half-hourly records; (B) solving Eq. 5.9 for the same data set and (C) solving Eq. 5.9 for all 3587 half-hourly periods between 1 January and 31 December 1995 with a dry canopy, $R_n > 100\ Wm^{-2}$, and functional instrumentation. Vertical bars represent ± one standard deviation.

the differences are non-significant. The predicted average diurnal pattern of r_s for all 3587 dry half-hourly periods of above-canopy climatic observations to which Eq. 5.9 could be applied (*i.e.* not during rainstorms or within 2 h after storms >1 mm; see section on rainfall) is displayed in Fig. 5.3C. Although the mean daytime values for r_s are generally higher compared to the previous predictions, the resulting pattern is very similar and was used in the remainder of the computations of λE.

Next, daily totals of E_t were calculated using Equations 5.3 and 5.9 for the same dry daytime hours. For periods characterized by a fully wetted canopy, r_s was set to zero and transpiration was assumed to have ceased [*Monteith*, 1965; *Rutter*, 1975]. It is recognized that the use of a 2-h threshold period for the canopy to dry up is arbitrary and may be conservative given the estimates of S and E_{wet} in Table 5.2. The computations were therefore repeated using a stop/go principle, with $r_s = 0$ for wet conditions using values of r_s as predicted by Eq. 5.9 immediately after rainfall had stopped. The effect of applying a threshold proved to be small (see below).

Equations 5.3 and 5.9 could be used on 233 days ($n = 3587$ half-hourly periods) for which there was a complete climatic record to compute daytime λE, the sum of which represents the evaporation from a dry canopy or transpiration (E_t). The total transpiration for this 233 *day*-period amounted to 354 mm or $1.52 \pm 0.73\ mm\,d^{-1}$ (maximum $4.36\ mm\,d^{-1}$; median $1.48\ mm\,d^{-1}$). Extrapolated to a period of 365 days would give an approximate annual E_t of 555 mm. Applying the stop/go principle without the use of a threshold period to allow the canopy to dry up, gave a total E_t for the 233 days of 363 mm (1.56 ± 0.70

$mm\,d^{-1}$), suggesting that the effect of applying a threshold period of 2 h is indeed small (*c.* 2.5 %).

Within the 132-*day* (*i.e.* 365 minus 233) data gap for daily E_t, 71 days had missing wind speed data. Therefore, daily E_t values (in $mm\,d^{-1}$) were related to the remaining climatic variables (notably mean daytime (06:00–18:00 h), R_n (Wm^{-2}), T ($^{\circ}C$), and RH (%)) using a multiple-regression analysis:

$$E_t = 8.90 + 0.005 \cdot R_n - 0.213 \cdot T - 0.058 \cdot RH \qquad (5.10)$$

Total E_t over the 304 days for which estimations could be made with reasonable reliability (by solving Eq. 5.3 and Eq. 5.10 for 233 and 71 days, respectively) amounted to 430 mm (equivalent to 516 $mm\,yr^{-1}$), or 1.41 ± 0.72 $mm\,d^{-1}$ (median: 1.35 $mm\,d^{-1}$). In the absence of climatic data collected at other locations in the vicinity of the study area that could have been used to help fill the remaining 61-*day* gap in the meteorological records, average values of 1.85 $mm\,d^{-1}$ and 1.03 $mm\,d^{-1}$ were adopted for the E_t of the 20 remaining dry days and 41 days with rain ($P > 0.44$ mm), respectively. These latter averages for dry and wet days were based on values obtained for 141 wet and 163 dry days during 1995.

Adding these 61 days to the total E_t for the 304 days gave an estimated annual E_t of 509 mm (1.39 ± 0.67 $mm\,d^{-1}$). The average reference open-water evaporation total according to *Penman* [1956] for the 365-*day* period was 3.0 ± 1.2 $mm\,d^{-1}$ (Section 4.4.3). Dividing the 1.4 $mm\,d^{-1}$ obtained for E_t (304 days) by the 3.0 $mm\,d^{-1}$ open-water evaporation E_0 (n = 318 days) gives an E_t:E_0 ratio of 0.47. This value is typical for montane forests that experience little or no cloud [*Bruijnzeel and Proctor*, 1995]. Using the stop/go principle referred to earlier, total E_t for the 365 days amounted to 526 mm. This represents an increase of 3.3 % compared to the computations in which a 2-h threshold period was applied to storms >1 mm. Not surprisingly, the effect was most pronounced on wet days for which average E_t of 1.11 $mm\,d^{-1}$ was obtained when no threshold was applied *vs.* 1.03 $mm\,d^{-1}$ for the computations using a 2-h threshold period.

In the absence of direct estimates of E_t for the PMull and MMor forests themselves, the value obtained for the regenerating forest at Bellevue Peak (509 $mm\,yr^{-1}$) may be used as a starting point. Although it is recognized that extrapolating the Bellevue Peak results to the two older forests has its limitations, no statistically significant differences were found in the weighted mean $\delta^{13}C$ concentrations in leaves collected in a series of mature sun leaves from four forests of gradually increasing stature in the study area, including the PMull and MMor forests. This suggests a comparable gas exchange capacity (including water vapour) at the leaf level for these forests [*Ehleringer*, 1993; *Williams and Ehleringer*, 1996]. In addition, no significant differences were found in terms of stomatal size and density and photosynthetic capacity (see Section 6.3.1; *cf. Tanner and Kapos* [1982], *Aylett* [1985]). Such findings suggest that differences in transpiration rates, at least per unit of leaf area, between forests of contrasting stature in the study area may well be limited and therefore will be determined mainly by differences in leaf area index (LAI). Although the

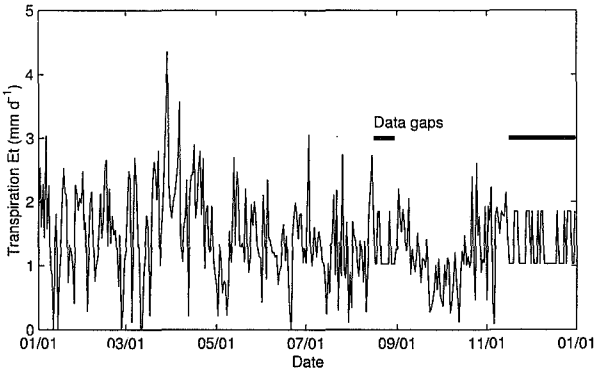

Figure 5.4: Daily transpiration totals for 1995 above regenerating forest vegetation at Bellevue Peak as determined with the Penman-Monteith evaporation model (233 days) and a multiple-regression equation (Eq. 5.10) between daily transpiration totals and pertinent climatic variables (71 days). Mean values for rainy and dry days (41 and 20 days; 1.02 *vs.* 1.85 $mm\,d^{-1}$) were used to estimate evaporation rates for the remaining gaps in the data (61 days).

Table 5.3: Annual amounts of rainfall (P), cloud water (CW), net precipitation (P_{net}), rainfall interception (E_i), transpiration (E_t), total evapotranspiration (ET), changes in soil water storage (ΔS), and drainage (D) beyond a 80 cm soil column in the PMull and MMor forests. Percentages of gross precipitation are given in parentheses.

Forest	P	CW	P_{net}	E_i	E_t	ET
PMull	3060	43 (1.4)	2632 (86)	428 (14)	620 (20.3)	1048 (34.2)
MMor	3060	104 (3.4)	2380 (78)	680 (22)	509 (16.6)	1189 (38.8)

Forest	ΔS	D
PMull	−20 (0.7)	2032 (66.4)
MMor	14 (0.5)	1857 (60.7)

LAI of the regenerating forest at Bellevue Peak is unknown, visual evidence suggests that it is similar to the LAI of the MMor (*c.* 4 m^2m^{-2}) but smaller than that of the PMull. The LAI of the MMor and PMull forests were estimated at 4.1 and 5.0 m^2m^{-2} (see Sections 2.3.1 and 4.4.3 for details). Taking the E_t value derived for the forest at Bellevue Peak (509 $mm\,yr^{-1}$) to represent that of the MMor forest, and adding the amount of intercepted rainfall E_i (680 mm), gives an estimated annual total evaporation (ET) of 1189 mm (Table 5.3). Taking the difference in LAI into account, the E_t for the PMull becomes about 620 $mm\,yr^{-1}$ (1.7 $mm\,d^{-1}$) and the ET about 1050 $mm\,yr^{-1}$ (Table 5.3). Needless to say, the values derived for the PMull forest in particular must be considered as approximations only.

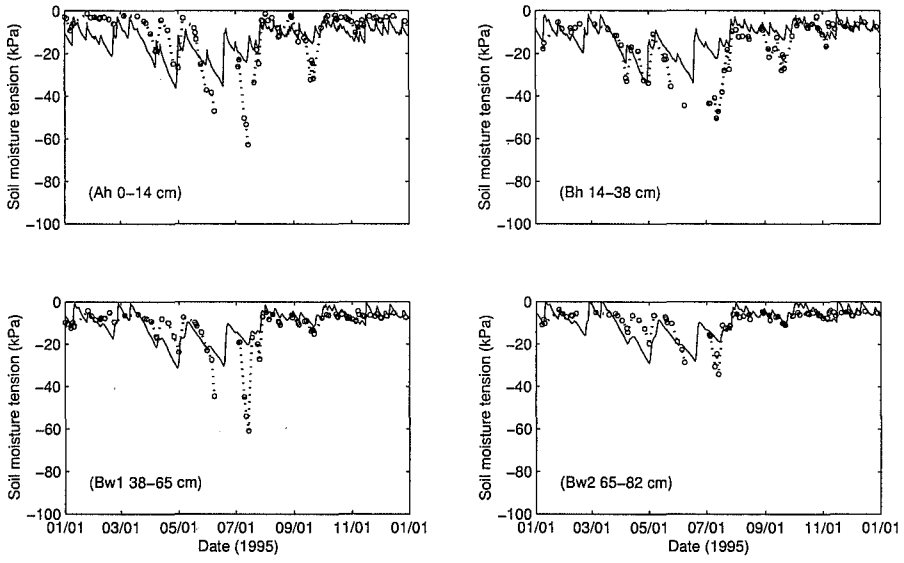

Figure 5.5: Observed (o) and predicted (solid line) values of soil moisture tensions (*kPa*) in the Ah (0–14 *cm*), Bh (14–38 *cm*), Bw1 (38–65 *cm*), and Bw2 (65–82 cm) horizons of the PMull forest soil in 1995.

5.5.4 Soil water dynamics

The soil water tension values (ψ_m) predicted by the VAMPS model are compared with actually measured values in the four main horizons of the PMull and MMor soils in Fig. 5.5 and Fig. 5.6, respectively. Apart from a consistent underestimation of moisture depletion from the thin uppermost soil horizon (Ah), the predicted patterns of ψ_m generally resemble those observed in the field. As indicated by Figs. 5.5 and 5.6, the soil underlying the MMor forest plot showed a higher sensitivity to drought than that of the PMull forest plot. Predicted values of ψ_m in the PMull soil never fell below -40 *kPa* at any depth but got below -60 *kPa* in the Ah and Bh horizons of the MMor soil during six days in April 1995 (including a predicted minimum ψ_m of -80 *kPa* in the Ah-horizon on 28 April. The lowest value of ψ_m observed in the field was -76 *kPa* (MMor Ah-horizon, 11 June 1995; Fig. 5.6).

The total amount of water draining beyond a depth of 80 *cm* was calculated at 2032 $mm\,yr^{-1}$ (66.4 % of P or 5.6 $mm\,d^{-1}$ on average) for the PMull plot *vs.* 1857 $mm\,yr^{-1}$ (60.7 % of P or 5.1 $mm\,d^{-1}$ on average) for the MMor plot. Overall changes in soil water storage (ΔS) in the two soil profiles were small: -20 *mm* (<0.7 % of P) for the PMull soil column and $+14$ *mm* (<0.5 % of P) for the MMor soil column (Table 5.3). It should be noted that the estimated contributions by CW were not taken into account in the model computations because the observed net precipitation totals already included net amounts of CW. As such, the computed soil water tensions and drainage amounts can

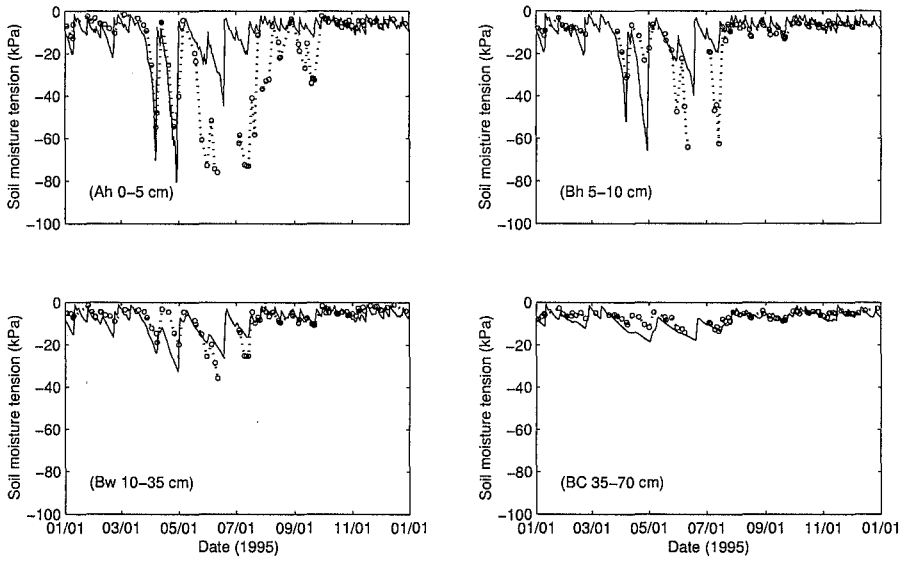

Figure 5.6: Observed (o) and predicted (solid line) values of soil moisture tensions (*kPa*) for the Ah (0–5 *cm*), Bh (5–10 *cm*), Bw (10–35 *cm*), and BC (35–$\simeq$70 *cm*) horizons of the MMor forest soil in over 1995.

hardly have been affected. Although the soil water dynamics in the two forest sites can be modelled reasonably well with VAMPS, it is difficult to assess the uncertainty associated with the outcome. However, considering the moderately successful simulation of soil water depletion patterns in the two forest plots in 1995, VAMPS was used to predict the number of days without precipitation that would be required to reach ψ_m values of -100 *kPa* ($pF = 3$, 'limiting point' where soil water stress starts to affect transpiration; *Landsberg* [1986]) and -1.58 *MPa* ($pF = 4.2$, 'permanent wilting point' where the vegetation starts to die) in an attempt to assess the relative sensitivity of the two forests to drought. The model was run with zero precipitation input and a constant transpiration rate of 1.83 $mm\,d^{-1}$ for the MMor forest and 2.23 $mm\,d^{-1}$ for the PMull as observed during dry days in the dry season (April–July) until a value of $\psi_m = -100$ *kPa* was reached. The simulations started with an average ψ_m profile as typically observed during the dry season (April–July). In the PMull profile a value of -100 *kPa* was reached after 37, 43, and 56 days for, successively, the Ah/Bh, Bw1 and Bw2 horizons, whereas 117, 134, and 248 days were required to reach the permanent wilting point in the Ah, Bh, and Bw1 horizons (0–65 *cm*). Conversely, in the MMor soil profile, a value of $pF = 3$ was already reached after only 13, 16, and 58 rainless days throughout the Ah-Bh-Bw horizons (0–35 *cm*) while permanent wilting point would be reached after approximately 40, 80, and 220 rainless days, respectively. The shallow rooting depth in the MMor profile [*Elbers*, 1996] prevented the BC-horizon (35–80 *cm*) from attaining values of $\psi_m \leq -120$ *kPa* within a one-year dry period.

5.6 DISCUSSION

5.6.1 NET RAINFALL AND RAINFALL INTERCEPTION

At 73 % and 60 % of incident rainfall, the relative amounts of throughfall (Tf) observed in the PMull and MMor forests during 1995 are rather different and, at first sight, contrary to expectations on the basis of the observed contrasts between measurements of below-canopy PAR levels (5 % *vs.* 13 % of incoming PAR; see Section 4.4.3) and LAI. However, the very low Tf value obtained for the MMor forest is partly explained by the very high stemflow (Sf) percentage (18.3 % *vs.* 13.0 % for the PMull site), bringing the sum of Tf and Sf to 86 % and 78 % for the PMull and MMor forest, respectively.

In a recent assessment of the hydrological characteristics of tropical montane forests *Bruijnzeel* [1999] distinguished three classes: (i) tall forest that is little affected by fog or low cloud (Tf typically 65–80 %; Sf<1 %); (ii) mossy forest of intermediate stature and variable cloud incidence (Tf 55–130 %; Sf usually <1 % but occasionally up to 10 %); and (iii) stunted ridge-top upper montane forest subject to frequent cloud (Tf 90–125 %; Sf 5–10 %). Comparison of the Jamaican results with the ranges reported for the respective forest types highlights a unique combination of high stemflow (typical for short-statured cloud-ridden forest) and low throughfall (typical for tall forest or epiphyte laden forest of intermediate stature; *Bruijnzeel* [1999]). Such findings once more suggest that adverse edaphic rather than adverse climatic conditions must be held responsible for the occurrence of short-statured forest in the study area (*cf.* Chapter 2; see also Section 5.6.4). Interestingly, a high stemflow percentage has also been reported for so-called lowland heath forest on infertile white sands in Amazonia [*Jordan*, 1978], which has a number of physiognomic conditions in common with low-statured montane forests [*Whitmore*, 1998]. However, our stemflow data should be interpreted with care because of their high spatial and temporal variability. Although variations in tree diameter and species were taken into account, errors are inevitably introduced when converting measured volumetric data to *mm* of water because of the difficulties associated with estimating the projected areas of the crowns of sample trees. A comparison of patterns of measured amounts of Sf with those predicted by the analytical model of interception over 1995 revealed that deviations did occur during a few storms >50 *mm* when several individual trees carried extreme volumes of Sf (*R. L. L. J. Hafkenscheid,*), *unpublished.*

The lack of agreement between measured rainfall interception values and differences in forest physiognomy (the stunted MMor forest has both the lowest LAI and the highest E_i) increases even further if contributions via cloud water interception are taken into account: from *c.* 250 *mm*(rainfall only) to *c.* 315 *mm* (rainfall plus cloud water; Table 5.3). This unexpected result, plus the discrepancy in optimized values for evaporation from a wet canopy between the two forest plots (Section 5.5.2) may well be related to errors in the measurements of net rainfall. Taking the total annual amounts of Tf caught by each of the 12 moving gauges per forest as an individual sample gave coefficients of

variation of 5.8 % for the PMull forest and 10.3 % for the MMor. The number of gauges required for accurate estimates of throughfall volumes (*e.g.* a coefficient of variance of 5 % or a confidence interval of 95 %) can be calculated following *Kimmins* [1973]:

$$\text{Required number of gauges} = \frac{t^2 \times \text{Coefficient of Variation}^2}{c^2} \qquad (5.11)$$

where t is the *student's-t* value for a desired confidence interval (c)(expressed as a percentage of the mean). Solving Eq. 5.11 for the observed CoV's (5.8 % for the PMull, 10.3 % for the MMor) and $t = 2.18$ (95 % confidence interval; *Spiegel* [1972]) suggests that 7 and 20 gauges would be required to obtain reliable Tf measurements for the PMull and MMor forest, respectively. It can be concluded therefore that 12 gauges were sufficient to sample Tf adequately in the PMull forest but quite insufficient in the MMor forest. These computations do not tale into account any error in the measurements of the stemflow component. Because the readings of individual stemflow gauges depend on species, size and shape of the trees to which they are attached it is not possible to assess the error associated with the stemflow measurements.

5.6.2 Transpiration

Quantitative information on water uptake (E_t) in tropical montane forests is scarce and mostly based on catchment water budgets, *i.e.* obtained by subtracting amounts of intercepted rainfall from total evapotranspiration ET. In view of the potentially large cumulative errors associated with such estimates [*cf.* *Lee*, 1970] the absence of any trends in the values of E_t or ET with elevation is not surprising [*Bruijnzeel*, 1990; *Bruijnzeel and Proctor*, 1995]. *Bruijnzeel and Proctor* [1995] suggested water-balance based values for E_t of 510–830 $mm\,yr^{-1}$ for tall montane rain forests that are little affected by fog and low cloud *vs.* 250–310 $mm\,yr^{-1}$ for (shorter-statured) mossy forests subject to frequent fog incidence. Therefore, at 509 $mm\,yr^{-1}$ (Table 5.3) the annual transpiration total derived for the regenerating forest at Bellevue Peak falls in the lower part of the reported range for (tall) montane forests below the main cloud belt and greatly exceeds values observed for 'true' cloud forest. This observation agrees with the small amounts of cloud water interception (1.4–3.4 % of annual P) that were derived for the PMull and MMor forests, respectively.

Compared to 'true' upper montane cloud forests, the high transpiration figure found in the present study becomes more pronounced when expressed as the ratio to the reference open-water evaporation according to *Penman* [1956] (E_0). The E_t:E_0 ratio reported for several tall montane forests experiencing little to no cloud ranges from 0.47–0.56 [*Bruijnzeel and Proctor*, 1995] and exactly span the presently obtained value of 0.47 ($E_t = 1.41\ mm\,d^{-1}$, $E_0 = 3.0\ mm\,d^{-1}$ for the regenerating forest at Bellevue Peak (and probably the MMor) and the 0.57 ($E_t = 1.70$) for the PMull forest.

Much lower E_t:E_0 ratios (0.22–0.25) have been reported for short-statured summit forests on cloud-affected coastal mountains of comparatively low elevation (700–1015 m) in South-east Asia [*Bruijnzeel et al.*, 1993; *Hafkenscheid*, 1994] and Puerto Rico [*Holwerda*, 1997]. Interestingly, these seemingly consistent ratios were obtained under quite contrasting evaporative conditions and rainfall regimes. Corresponding values of E_0 varied between 1.9 $mm\,d^{-1}$ at the Puerto Rican site and 3.6–4.9 $mm\,d^{-1}$ at the South-east asian sites. Also, rainfall and cloud incidence at the latter locations occur mainly in the afternoon (as in Jamaica (Fig. 4.2)) but falls largely at night and in the early morning in Puerto Rico [*Schellekens et al.*, 1998].

Such contrasts further support the contention that the forests of the present study cannot be regarded as 'true' cloud forests, *i.e.* characterized by high cloud water interception and low transpiration [*Stadtmüller*, 1987]. It remains to be seen, however, whether the rates of E_t derived above the regenerating vegetation at Bellevue Peak apply equally to the older-growth forests. On the other hand, as indicated earlier, no systematic differences were found in the δ^{13} C values for the leaves of seven principal tree species in four forest plots of gradually decreasing stature on increasingly acid soils in the study area, including the PMull and MMor sites (Section 6.3.2). Given the fact that δ^{13} C values are determined by the ratio of intercellular and atmospheric partial CO_2 pressures, the observed similarity in values for tall and stunted forest could imply a comparable gas exchange capacity, including for water vapour. This, together with the close correlation between atmospheric saturation deficits and foliar δ^{13} C concentrations [*Kitayama et al.*, 1998], the presumably identical ambient climatic conditions and partial CO_2 pressures experienced by the nearly adjacent PMull and MMor forests, and the absence of significant inter-site differences in stomatal density and size (Table 6.6) all suggest that contrasts in transpiration rates per unit leaf area between the different forest types in the study area is probably limited. Additional studies of water uptake in the PMull and MMor forests are required to confirm to what extent extrapolation of the results obtained at Bellevue Peak to the two forests was justified. In view of the difficulties encountered with operating heat pulse velocity equipment at the study sites due to the prevailing high humidity levels, future studies could consider employing isotope injection techniques [*Calder*, 1992; *Dye et al.*, 1992] as an alternative. Finally, the LAI of the forest at Bellevue Peak will need to be known as well to further assess the degree of discrepancy in E_t between young and old-growth forests in the area.

5.6.3 Evapotranspiration

The annual estimates of evaporation (ET) for the PMull and MMor forests listed in Table 5.3 (1050 and 1190 $mm\,yr^{-1}$, respectively) must be considered preliminary in view of the extrapolation of the transpiration results for the regenerating forest at Bellevue Peak to the forest plots. Not surprisingly in view of the rather high values obtained for E_t (510–620 $mm\,yr^{-1}$), the presently derived annual totals for ET fall in the range reported for tall montane forest

not affected by cloud [*Bruijnzeel*, 1999]. It is of interest to note that elsewhere in Jamaica *Richardson* [1982] established a value of 2000 $mm\,yr^{-1}$ for the ET of a rain forested catchment at 775–1265 m a.s.l. using the water balance technique. Although this value may have been influenced by deep leakage (J. H. Richardson, *personal communication* to L. A. Bruijnzeel) there are several recent studies of forest evaporation at mostly wet maritime tropical locations that have also reported much higher values of ET (1770–2400; *Malmer* [1993], *Waterloo et al.* [1999], *Schellekens et al.* [2000]) than the 1300–1500 mm normally found for lowland rain forest [*Bruijnzeel*, 1990]. However, it cannot be concluded from such observations that the presently derived high evaporation totals could also have been obtained because of the specific climatic conditions prevailing at the study site. The high E_t totals reported for other wet maritime locations (Puerto Rico, East Malaysia) were largely caused by high rainfall interception [*Malmer*, 1993; *Schellekens et al.*, 2000] whereas in the present case E_t is equally important (Table 5.3).

5.6.4 Soil water regime

As shown in Fig. 5.5 and Fig. 5.6, the soils of the study sites were never waterlogged and only occasionally experienced high, but not critical, soil water tensions. Although montane forest on shallow soils has been reported to be dying following severe drought [*Lowry et al.*, 1973; *Werner*, 1988], *Bruijnzeel et al.* [1993] demonstrated that an extreme drought in East Malaysia did not cause increased leaf shedding in forest frequently enveloped in cloud whereas forests below the cloud zone were significantly affected. Similarly, a severe drought occurring in 1993–1994 in Puerto Rico did not affect soil moisture levels in stunted 'elfin' cloud forest (F. N. Scatena, *personal communication*). The rejection by *Bruijnzeel et al.* [1993] of regular soil water deficiency as a major factor governing the distribution of low-statured montane forest is also supported by the work of *Kapos and Tanner* [1985] in the study area where, during 1.5 years of soil water observations in Mor and Mull forests, topsoil water tensions always remained above -1.50 MPa, and therefore did not reach permanent wilting point. More importantly, soil water tensions in Mull forest soil were consistently higher than in Mor soil [*Kapos and Tanner*, 1985].

The simulations with the VAMPS model indicated that in the more shallow MMor soil tensions below -100 kPa ($pF = 3$) may be expected down to a depth of 25 cm after 58 rainless days (16 days for the top 10 cm) whereas permanent wilting point would be reached after approximately 220 dry days (80 days for the top 10 cm). Conversely, in the deeper PMull soil it would take 37–56 rain-free days to reach $\psi_m \leq -100$ kPa in the top 15 to 40 cm and 117–134 dry days to reach wilting point (depending on soil horizon depth). Naturally, these results depend strongly on the adopted rates of water extraction (2.23 $mm\,d^{-1}$ for the PMull; 1.83 $mm\,d^{-1}$ for the MMor) which were based on the observations made for young forest on Bellevue Peak.

Examination of the historic rainfall data at nearby Cinchona (1500 m a.s.l.) indicates that long dry spells are rare but possible. Between 1901 and 1990, 16

months with rainfall <10 *mm* have been identified whereas two long dry periods occurred, viz. 30 days in 1986 and 39 days in 1987 (J. R. Healey, *personal communication*). However, rainfall at Cinchona, which is situated in a more leeward position and at a lower elevation than the study plots (*cf.* Fig. 2.1 in Chapter 2), is probably lower than that at Bellevue Peak [*cf. Tanner*, 1980a]. During ordinary years severe soil water stress is probably absent and, as such, not important in determining stature and physiognomy of the forests in the study area. However, rare occasional drought will primarily affect the forest growing on shallow Mor soils. Adverse effects of such long dry spells on the growth of the Mor type forest can therefore not be ruled out entirely.

As most observations of soil water dynamics and leaf water potential in upper montane forests indicate wet to very wet conditions, with little chance that the trees will ever experience severe soil water deficits [*Lyford*, 1969; *Herrmann*, 1971; *Hetsch and Hoheisel*, 1976; *Dohrenwend*, 1979; *Bruijnzeel et al.*, 1993], waterlogging and subsequent root anoxia have been advanced as contributing to the development of forests that are limited in growth. *Hetsch and Hoheisel* [1976] in Venezuela and *Santiago et al.* [1999] in Hawaii reported clear negative relationships between montane forest stature, leaf area and the degree of soil saturation. However, persistent waterlogging is not necessarily a characteristic of all stunted tropical montane forests [*Kapos and Tanner*, 1985; *Hafkenscheid*, 1994]. Despite the occasional occurrence of exceptional amounts of rainfall (*e.g.* more than 1200 *mm* in 5 days in February 1996), the soils in the study forests never became waterlogged because the high permeability of the soils prevented fully saturated conditions. In conclusion, waterlogging is not an important factor governing forest stature in the study area [*cf. Kapos and Tanner*, 1985].

5.7 Conclusions

Amounts of cloud water interception by the MMor and PMull forest are low and insufficient to play an important role in the overall forest water balance or explain differences in stature. The full implications of cloud water interception on leaf physiological behaviour, notably a reduction of transpiration and photosynthetic activity, are as yet unknown but there are indications that such effects are small, or at least not more pronounced in the stunted MMor forest than in the taller-statured PMull forest (*cf.* Section 6.3.2). The relative magnitude of net precipitation (throughfall + stemflow) in the PMull and MMor forests (250 *mm* higher in the PMull) suggest that the depth of net precipitation in the low-statured MMor forest is likely to have been underestimated. However, the error associated with the measurements of Tf alone (± 6 % and 10 % of the mean in the PMull and MMor, respectively) cannot explain the discrepancy, implying that errors in the measurements of stemflow (notably in the MMor forest) are important as well. The specific physiognomy of Mor-type forest (numerous trees with multiple stems, gnarled appearance of trunks and branches festooned with mosses and epiphytes, etc.) probably demand a much higher number of Tf (and Sf) gauges than used in the present study (*cf.* Eq. 5.11)

The estimated rates of transpiration (E_t) in the two forests are not particularly low and, judged against the overall atmospheric conditions, comparable to values reported for tall montane forests that experience little or no cloud. The current assumption that the E_t determined for the regenerating forest at Bellevue Peak represents transpiration in the MMor forest as well requires validation, for example by a rerun of the sapflow measurements (after redesigning the equipment) or by employing isotope injection techniques.

Soil characteristics prevent prolonged soil saturation in both the PMull and MMor forest; persistent water logging or root anoxia therefore cannot be an important factor governing the stature and physiognomy of these forests. Contrasts in soil water holding capacity and rooting depth (both less in the MMor) suggest that the MMor forest may be more sensitive to the effects of occasional drought (which are rare but do occur in the area) than the forests growing on the deeper Mull soils. However, simulation of the effects of prolonged dry spells on soil water levels and thus the long-term functioning of the forests suggested drought to have a minimal effect. Longer-term monitoring of soil water status in combination with weekly litterfall observations would be desirable to test this contention.

In conclusion: the present hydrological results suggest that unfavourable (non-physical) edaphic conditions (such as high acidity, excess aluminium, and low key nutrients) may be held responsible for the low above-ground productivity and stature observed in the more stunted forest types in the study area.

6

PHOTOSYNTHETIC, ISOTOPIC AND STOMATAL CHARACTERISTICS OF PRINCIPAL TREE SPECIES IN MONTANE FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS OF JAMAICA*

ABSTRACT

Despite being subject to apparently similar geological and climatological conditions and showing considerable overlap in species composition, montane forests in the Blue Mountains, Jamaica, exhibit striking contrasts in soil humus development, ecological functioning, and tree physiognomy, notably tree stature (7–17 m). We tested the hypothesis that the differences in stature are related to contrasts in photosynthetic capacity. Logistic limitations prevented long-term measurements of actual photosynthesis under local light conditions. Instead, light-saturated photosynthetic rates (A_{max}) were measured on leaves of seven principal tree species from a sequence of four forests showing a gradual reduction in tree height from well-developed 'Mull' forest (main canopy height 12–17 m, tree LAI = 5.1) to stunted 'Mor' forests (5–8 m, tree LAI = 4.1). Rank-sum tests for multiple populations showed no significant differences between forest types for any of the examined components, including A_{max}, foliar nitrogen, specific leaf mass, isotopic composition (δ^{13} C) and minimum stomatal resistance as modelled from stomatal traits. Differences between individual species, however, were significant for all parameters. A_{max} ranged from 9.4 $\mu mol\, m^{-2}\, s^{-1}$ for Cyrilla racemiflora to 3.4 for Chaetocarpus globosus; foliar N varied from 1.0 $g\, m^{-2}$ (Clethra occidentalis) to 2.4 (C. globosus and Alchornea latifolia) and δ^{13} C values between −27.0 (Clusia cf. havetioides) to −31.1 for C. occidentalis. The potential stomatal resistance ranged from 21.1 $s\, m^{-1}$ (C. havetioides) to 49.9 $s\, m^{-1}$ (Vaccinium meridionale). None of the examined parameters consistently mirrored the forest sequence based on main tree stature. Low productivity as a result of reduced leaf and canopy photosynthetic capacity and, consequently, reduced tree growth in the shorter-statured forests could, therefore, not be demonstrated.

*With: E. J. Veneklaas and L. A. Bruijnzeel. A shortened version of this chapter will be submitted to *Biotropica*.

6.1 INTRODUCTION

Tropical montane rain forests (TMRF) and lowland rain forests differ markedly with respect to their structure and physiognomy (notably canopy height, leaf mass, dominant leaf size, and relative amounts of above- and below-ground biomass) as well as in their ecological functioning (above- and below-ground productivity, transpiration, mineralization of organic matter) [*Grubb*, 1977; *Whitmore*, 1998; *Bruijnzeel and Veneklaas*, 1998].

With increasing elevation, the stature of the forest decreases and the leaves become both smaller, thicker, and harder (more 'xeromorphic') [*Grubb*, 1977]. The reduction in montane forest stature, referred to as 'forest stunting' in extreme cases, has received much attention but the phenomenon has remained largely unexplained. Over the years a variety of sometimes mutually contradicting hypotheses have been advanced, including: (i) soil moisture stress, either as a result of periodic drought or anaerobiosis in persistently saturated soils, (ii) reduced leaf temperatures and photosynthesis as a result of low temperatures and radiation inputs, (iii) nutrient limitation due to (a) inherently low soil fertility and high acidity of the substrate, or impaired root functioning, (b) reduced decomposition and mineralization rates, or (c) low uptake capacity due to climatically reduced transpiration rates [*Grubb*, 1977; *Bruijnzeel and Proctor*, 1995; *Bruijnzeel and Veneklaas*, 1998; *Silver et al.*, 1999].

The zonation of montane forests, their physiognomy and the apparently low productivity of low-statured upper montane rain forests have been associated with frequently occurring or persistent fog and low cloud [*Grubb et al.*, 1963]. Generally speaking, the reduction in radiation flux density and air/leaf temperatures, the increase in atmospheric humidity and the more prolonged leaf wetness associated with fog, all tend to have an attenuating effect on transpiration and photosynthetic activity in these so-called tropical montane cloud forests, compared to lowland forests or montane forests less affected by cloud [*Grubb*, 1977; *Steinhardt*, 1979; *Tanner*, 1980a; *Kapos and Tanner*, 1985; *Ishibashi and Terashima*, 1995; *Bruijnzeel and Veneklaas*, 1998].

A second factor determining forest productivity concerns the distribution of leaf area. Montane forests affected by cloud tend to have similar leaf mass, smaller above-ground woody biomass but similar or higher root biomass than lowland rain forests or montane forests below the cloud belt [*Grubb*, 1977; *Medina and Klinge*, 1983; *Weaver et al.*, 1986; *Cavelier*, 1989]. Because leaf mass per unit area is usually increased in montane forests (*i.e.* the leaves are thicker, particularly in short-statured upper montane forests), the leaf area index (LAI) of such forests is generally reduced and this results in lower productivity per unit leaf area [*Bruijnzeel and Veneklaas*, 1998]. The lower productivity of tropical montane (cloud) forest compared to lowland forests also manifests itself as lower litterfall and stem increment values [*Brown*, 1919; *Weaver et al.*, 1986; *Tanner*, 1980a, b; *Weaver et al.*, 1986; *Proctor et al.*, 1988, 1989].

The comparison of site conditions and ecological processes is usually hampered by the fact that forests of contrasting stature along an elevational gradient are not only subject to concurrent changes in soil type and climatic conditions but normally they also differ floristically [*Proctor et al.*, 1988, 1989; *Veneklaas and Van Ek*, 1990; *Pendry and Proctor*, 1996a, b; *Liebermann et al.*, 1996]. There is merit, therefore, in a 'lateral' comparison of forests of contrasting stature but subject to the same climatic and geological conditions. *Grubb and Tanner* [1976] described a sequence of mostly upper montane forests at 1600–1800 *m* a.s.l. along a ridge between John Crow Peak and Sir John Peak in the Blue Mountains of Jamaica. Whilst these forests show marked contrasts in canopy height (ranging from 5–7 *m* to 13–17 *m*), they also have a considerable overlap in species composition. The overall climatic conditions experienced by these different forests are comparable but their humus development differs [*Tanner*, 1977a, b]. These contrasts in stature have previously been attributed to differences in atmospheric humidity (notably exposure to fog incidence) [*Shreve*, 1914] or contrasts in soil fertility [*Tanner*, 1977a, 1985; *Healey*, 1990]. *Bruijnzeel* [1989b] drew attention to the fact that annual additions of nutrients via rainfall [*Tanner*, 1977b] greatly exceeded the corresponding amounts taken up and immobilized in the trunks of these forests [*Tanner*, 1985]. *Bruijnzeel et al.* [1993] observed a similar discrepancy in a stunted montane forest in East Malaysia and suggested that high concentrations of phenolic substances leached into the soil might interfere with photosynthesis, cell division in the fine roots, and ion uptake.

This paper examines the possibility that the contrasts in forest stature and tree physiognomy observed in the Jamaican situation can be explained by intrinsic differences in photosynthetic capacity. We have chosen to restrict the comparison between forest types to measurements of maximum photosynthesis at high light intensities to limit variations due to differences in the natural light climate, diurnal trends, and changing weather conditions during the measurements. In addition, stomatal characteristics, foliar nitrogen concentrations and carbon isotope composition were determined to support the interpretation of possible differences in photosynthetic capacity.

6.2 Materials and methods

6.2.1 Study area

Tanner [1977a] described a series of (largely upper) montane ridge top forest types at an elevation of *c.* 1600 *m* a.s.l. between John Crow Peak and Sir John Peak. The 'end members' of this series consisted of relatively tall (13–17 *m*) 'well-developed' Mull forest (WMull) and short-statured (5–7 *m*) Mor forest. Two additional upper montane forests of contrasting stature were selected by the present project on a SW-orientated spur between Sir John Peak and Bellevue Peak (1849 *m* a.s.l.), the distance between the latter and the sites being less than 150 *m* (see Fig. 2.1 in Chapter 2 for locations of all four plots). The shorter of the two forests is situated at 1824 *m* a.s.l. on a freely exposed ridge top

and was classified as 'moderately-developed' Mor forest (MMor, main canopy height 5–8 m). The taller (7–12 m) forest of the two is located on an almost level section of the NW slope of the same ridge at an elevation of 1809 m and was classified as a 'poorly-developed' Mull forest (PMull). As such, the two additional plots are considered to represent intermediate stages in the Mor to WMull forest sequence. The lateral distance between the two forests is less than 30 m. Although the PMull and MMor forest plots are located at slightly higher elevations (1809–1824 m) than the Mor and WMull forest plots described by *Tanner* [1977a], any climatic differences (in particular radiation flux densities) are considered to be small [*cf.* *Aylett*, 1985, ; Section 4.4.3].

A tabular overview of basic forest structural characteristics of the four forest plots (WMull, PMull, MMor, Mor) is given in Table 6.1. An extensive description of their floristics and edaphic conditions has been presented in Chapter 2 whereas the climatic conditions during 1995 as well as the hydrological functioning of the MMor and PMull forests were discussed in Chapters 4 and 5, respectively. Summarizing, the soils of the study plots have low nutrient concentrations and the pH of the ectorganic and topsoil horizons show a distinct gradient that mirrors the reduction in tree stature in the sequence WMull>PMull>MMor≥Mor. Precipitation in the study area is unevenly distributed over the year and amounts to *c.* 2850 $mm\,yr^{-1}$ but inter-annual differences may be considerable. The months March and July are usually relatively dry (rainfall < 90 mm per month as measured at nearby Cinchona, 1500 m a.s.l., *cf.* Fig. 2.1) whereas October and November are normally very wet (> 350 mm per month). In 1995, which was slightly wetter than normal, 327 separate rainfall events were measured at Bellevue Peak, distributed over 205 days with rain > 0.44 mm. Median event-based rainfall amount and duration in 1995 were 1.78 mm and 00:40 h. Most of the rain was recorded during the day, whereas the nights and early mornings were usually dry. During 1995, 71 dry periods of at least 24 h were recorded, of which 51 (72 %) lasted less than 48 h. The longest consecutive dry period lasted 11 days (Section 4.4.1). Annual deposition of fog was estimated at 43 mm (PMull) and 104 mm (MMor), or 1.4 and 3.4 % of the corresponding rainfall (Section 4.4.2).

Typical average daytime photosynthetic photonflux densities (*PPFD*) are *c.* 1150 and 260 $\mu mol\,m^{-2}\,d^{-1}$ for sunny and clouded conditions, respectively. Maximum fluxes of >2000 $\mu mol\,m^{-2}\,s^{-1}$ and <500 $\mu mol\,m^{-2}\,s^{-1}$ are experienced around midday, depending on cloud cover. The mean daytime (06:00 – 18:00 h) temperature as measured at 50 cm above a low regenerating forest canopy at Bellevue Peak (1849 m a.s.l.) was *c.* 17 $^{\circ}C$; relative humidity averaged 85 % with a typical diurnal range between 80 % in the early morning and 90 % around 18:00 h. Wind speeds averaged 3.1 $m\,s^{-1}$, increasing to 5.5 $m\,s^{-1}$ during the night. The average reference evaporation rate E_0 [*Penman*, 1956] was estimated at 3.0 $mm\,d^{-1}$ and ranged from 0.4 to 8.4 $mm\,d^{-1}$, depending on cloud cover (Section 4.4.3). The dominant leaf size is microphyllous to notophyllous and the leaves are hard and leathery [*Tanner and Kapos*, 1982]. The seven principal native tree species are listed in Table 2.2.

Table 6.1: Species richness per plot, total tree basal area (BA), main canopy height, density of trees and the number of trees with multiple trunks (TWMT) per unit area (*ha*), specific leaf area (SLA) and tree leaf area index (LAI) in the four forest types.

Forest	Species per site	BA $m^2\,ha^{-1}$	Height m	Trees ha^{-1}	TWMT ha^{-1}	Trunk/tree ratio	SLA $cm^2\,g^{-1}$	LAI -
WMull	34	77.9	13–17	6200	175	1.03	92	5.1[1]
PMull	23	53.1	7–12	4400	567	1.19	60	5.0[3]
MMor	10	44.4	5–8	6043	1043	1.29	61	4.1[2]
Mor	16	64.7	5–7	4900	1500	1.49	60	4.1[1]

Enumeration criteria for Mor and WMull: diameter at breast height (d.b.h.) $\geq$3.2 *cm*; for MMor and PMull: d.b.h. $\geq$5 *cm*. Data for the Mor and WMull sites: *Tanner* [1977a, 1980b, a] and E. V. J. Tanner, *personal communication*, 1996. Plot sizes are 0.10, 0.03, 0.024, and 0.08 *ha* for the WMull, PMull, MMor, and Mor, respectively.
[1]based on destructive sampling [*Tanner*, 1980b]; [2]based on litterfall rates and SLA (*cf.* Section 2.3.1); [3]based on measurements of below-canopy PAR (*cf.* Section 4.4.3).

Table 6.2: The percentage contributions of seven principal tree species to total plot basal areas (BA) in the four forest types Total BA in Table 6.1.

Species	Mor	MMor	PMull	WMull
	BA (%)			
Alchornea latifolia (Euphorbiaceae)	9.9	0.7	15.1	5.5
Chaetocarpus globosus (Euphorbiaceae)	17.0	8.9	16.0	4.8
Clethra occidentalis (Clethraceae)	3.8	5.7	6.3	21.7
Clusia cf. *havetioides* (Clusiaceae)	9.3	3.3	1.6	0.1
Cyrilla racemiflora (Cyrillaceae)	13.7	23.4	20.0	21.9
Lyonia cf. *octandra* (Ericaceae)	36.8	45.5	12.7	4.9
Vaccinium meridionale (Ericaceae)	2.8	6.6	1.8	2.3
others	6.7	5.9	26.5	38.8

Data for the Mor and WMull forests were taken from *Tanner* [1977a]; those for the MMor and PMull forest from Table 2.2. Nomenclature according to *Adams* [1972].

6.2.2 METHODOLOGY

All measurements concentrated on the seven principal species listed in Table 6.2. Photosynthetic rates were measured in the field between 19 and 27 March 1996 using the ADC LCA2 portable system (broadleaf chamber, window size 25×25 mm). CO_2 uptake was measured as the difference between inflowing and outflowing air of a test chamber in which a leaf was exposed to a light source. Fully exposed branches from the upper crown area of the trees were cut, placed in water containers, and immediately re-cut under water in order to maintain a continuous water column in the xylem vessels. At least six mature, but non-senescent leaves for each of the seven principal species were randomly selected for measurement. Individual leaves that were damaged by herbivory, discoloured, or having abnormal dimensions were left out but not removed. Measurements were performed within 10 *min* after collection. Because the Mor and WMull plots are permanent research locations, sampling in those forest types was restricted to areas adjacent to the original plots in order to minimize disturbance. During most of the measurements overcast weather conditions were experienced. Therefore, a 50 W halogen light source powered by car batteries was used to guarantee a *PPFD* of 1000 $\mu mol\, m^{-2}\, s^{-1}$ at the leaf surface. Previous work by *Aylett* [1985] in the area has indicated that the leaves of *Clethra occidentalis* and *Lyonia* cf. *octandra* become light-saturated at *PPFD* levels $> 500\ \mu mol\, m^{-2}\, s^{-1}$. Maximum photosynthetic rates were expressed on a leaf-area or dry-weight basis and denoted A^a_{max} ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$) and A^m_{max}($\mu\, mol\, CO_2\, kg^{-1}\, s^{-1}$), respectively. Leaf discs (6 mm diameter) were used to calculate leaf mass per area (LMA); the central veins were included in the discs. Rates of dark respiration (R_d) for each species were determined on leaves attached to large, freshly cut branches after acclimatisation in the dark for 15 to 90 *min*. The branches were collected in the late afternoon in the Mor and WMull area, re-cut under water and transferred to the Cinchona field station (elevation 1500 m) where the measurements were made in the evening. Logistical constraints prevented measurements of dark respiration to be made for all four individual plots.

The natural abundance of ^{13}C in C_3 plants is basically determined by the isotopic composition of the source CO_2 and isotopic discrimination during photosynthetic gas exchange. The major components contributing to the isotopic effect of the latter are (i) the discrimination associated with the differential diffusivity of $^{12}CO_2$ and $^{13}CO_2$ and (ii) the enzyme fractionation during carboxylation. The carbon isotope discrimination Δ is partly determined by the ratio of intercellular to atmospheric CO_2 pressure (p_i/p_a) and is, in its simplest form, described by:

$$\Delta = a + (b - a) \cdot \frac{p_i}{p_a} \tag{6.1}$$

where a is the fractionation due to diffusion of air (4.4 ‰), and b the net fractionation by carboxylation (approximately 27 ‰; *Farquhar et al.* [1982, 1989]; *Comstock and Ehleringer* [1993]; *Williams and Ehleringer* [1996]). Values of p_i/p_a therefore represent the balance point between physical and biochemical constraints on photosynthetic capacity [*Williams and Ehleringer*, 1996]. Keeping all other factors constant (primarily the carboxylation capacity and the

composition of the source CO_2), any differences in p_i/p_a between plants are controlled by stomatal conductance [*Farquhar et al.*, 1989; *Kitayama et al.*, 1998]. Stable carbon isotope composition therefore allows the evaluation of the long-term, integrated effects of eco-physiological processes on stomatal response and behaviour of the photosynthetic apparatus [*Ehleringer*, 1989; *Pearcy et al.*, 1989]. Carbon isotope composition δ^{13} C was determined on oven-dried (24 h at 80 $^{\circ}C$) discs of foliar tissue (6 mm diameter). Samples were destructed by flash combustion. Isotopic composition (δ^{13} C) of the produced CO_2 was measured by continuous flow isotope ratio mass spectrometry (Europa Scientific Roboprep-Tracermass; Crewe, UK) using an internal standard (sugar beet, δ^{13} C = -25.96). The discrimination values Δ were calculated from the carbon isotopic ratios for the plant material and the ambient air (δ_{air}) following *Farquhar et al.* [1989].

With CO_2 and water vapour sharing the same stomata, stomatal characteristics that determine contrasts in Δ may provide insight in stomatal response to a variety of stresses, including soil water limitation [*Ehleringer*, 1993; *Williams and Ehleringer*, 1996]. In order to gain additional information on the potential gas exchange capacity of the respective species, their stomatal characteristics were determined on leaves from the cut branches. Sampling, again, was random but the restrictions mentioned previously were maintained. Foliar tissue was stored at 4 $^{\circ}C$ in a formaldehyde-acetic acid-ethanol mixture (FAA) until analysis. The samples were analyzed for stomatal size and stomatal density per unit area using lacquer impressions retrieved from the mid-leaf sections (including the mid-rib and major veins). Leaves from *Clethra occidentalis* could not be examined using this method because of its heavily tomentose lower epidermis [*Tanner and Kapos*, 1982]. For the remaining six species, stomatal density and length were determined microscopically for eight, randomly chosen, fields (0.5 × 0.5 mm, magnification 200 ×) on five leaves per species per plot. The length of the guard cells (L) was determined at 1000 × for twenty stomata per field. Two leaves per species per plot were examined for stomata on both leaf sides rather than the bottom side only.

In an attempt to capture stomatal behaviour in a single figure, a 'minimum stomatal resistance' was derived using the equation of *Monteith and Unsworth* [1990]:

$$r_{sto}^{min} = \frac{4(l + \pi d/8)}{\pi n D d^2} \tag{6.2}$$

where l is the depth of the stomatal tube, d the mean diameter of a circular pore, n the stomatal density and D the diffusion coefficient. The latter depends on atmospheric pressure and temperature and is approximately $28.5 \cdot 10^{-5}$ m^2 s^{-1} for water vapour at 17 $^{\circ}C$ and 85 kPa. The depth of the stomatal tube l was assumed to be approximated by the thickness of the lower epidermis, the values of which were taken from *Tanner and Kapos* [1982] (as were all other stomatal traits for *Clethra occidentalis*). Since the pores are elliptical rather than circular, d was estimated as $\sqrt{0.5} \cdot L$ as the maximum opening width was assumed to be half the guard cell length L. Total foliar nitrogen was measured using a CHN elemental analyzer (Perkin-Elmer 6500).

6.2.3 Statistics

As the sample sizes for the respective parameters varied and criteria for randomized sample collection could not be guaranteed during the field measurements, all data were analyzed using distribution-free or non-parametric statistics. Contrasts between plots were analyzed under the assumption of non-select and independent observations and equal frequency distributions (with the number of observations being seven, *i.e.* the number of species) using rank-sum tests for four populations (the four forest plots) [*Natrella*, 1963]. For species the number of observations is four with a population size of seven. Finally, the degree of dominance of certain species was analyzed using rank-sum maximum statistics [*Sachs*, 1970].

6.3 Results

6.3.1 Maximum carbon assimilation and dark respiration rates

The mean maximum net carbon assimilation rates per unit leaf area and mass for the seven principal tree species per forest type are given in Table 6.3 along with the corresponding values for foliar nitrogen concentration, specific leaf mass, and isotopic characteristics. Photosynthetic rates per unit leaf area (A^a_{max}) of leaves exposed to a *PPFD* of *c.* 1000 $\mu mol\, m^{-2}\, s^{-1}$ ranged from 3.44 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ for *Chaetocarpus globosus* to 9.39 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ for *Cyrilla racemiflora*. For none of the examined species there was evidence that maximum net photosynthesis on a leaf area basis was systematically lower in the more stunted Mor-type forests than in the taller-statured Mull-types. Using the rank-sum test for multiple populations [*Natrella*, 1963] with $n = 4$ (plots) for seven populations (species), the observed contrasts in A^a_{max} between species were found to be highly significant ($\alpha = 0.005$). In addition, rank-sum-maximum tests for dominance [*Sachs*, 1970] suggest that rates of A^a_{max} were significantly highest for *Cyrilla racemiflora* and lowest for *Chaetocarpus globosus* (Table 6.7). Therefore, average values for the respective parameters can be expected to differ per forest type, depending on their floristic composition. Single plot averages were computed from the values for the individual species using a weighting procedure based on the relative contribution to plot basal area of each species. The resulting averages are given in Table 6.4.

Converting the maximum carbon assimilation rates per unit leaf area for the respective species to rates per unit leaf mass (A^m_{max}) did not reveal any trend between forest types either (Table 6.3). Being the quotient of A^a_{max} and leaf mass per unit area (LMA) A^m_{max} varied in different directions for different species as an increase in LMA was associated with a reduction in forest stature for *Chaetocarpus globosus*, *Cyrilla racemiflora*, and *Lyonia* cf. *octandra* but not for the other species (Table 6.3). However, the plot-based averages of A^m_{max} did parallel the contrasts in stature between the forest types, with the highest values for the WMull and the lowest for the Mor forest (Table 6.4). The mean LMA for *Clethra occidentalis* (0.10 $kg\, m^{-2}$) and *Clusia* cf. *havetioides* (0.37 $kg\, m^{-2}$)

Table 6.3: Maximum carbon assimilation rates per unit leaf area (A^a_{max}, $\mu mol\,CO_2\,m^{-2}\,s^{-1}$) and mass ($A^m_{max}$, $\mu\,mol\,CO_2\,kg^{-1}\,s^{-1}$), total nitrogen concentration (N, $mg\,g^{-1}$ and $mg\,m^{-2}$), leaf mass per unit area (LMA, $kg\,m^{-2}$), carbon isotope composition (δ^{13} C) and discrimination (Δ), and estimates of the ratio between intercellular to atmospheric CO_2 pressure (p_i/p_a) for foliage of seven principal tree species in the Mor, MMor, PMull, and WMull forest types.

Forest	Species	LMA $[kg\,m^{-2}]$	A^a_{max}	A^m_{max}	N $[mg\,g^{-1}]$	N $[g\,m^{-2}]$	δ^{13} C [-]	Δ [-]	p_i/p_a [-]
Mor	*A. latifolia*	0.183	5.53	30.2	14.8	2.72	-27.3	20.15	0.75
MMor		0.164	5.85	35.6	13.4	2.20	-27.8	20.68	0.77
PMull		0.156	5.63	35.2	15.3	2.39	-26.0	18.79	0.70
WMull		0.177	8.54	48.2	12.3	2.18	-27.0	19.84	0.73
Mor	*C. globosus*	0.274	5.40	19.9	9.0	2.47	-29.5	22.46	0.83
MMor		0.272	4.22	15.5	9.0	2.45	-27.9	20.78	0.70
PMull		0.220	3.44	15.6	10.8	2.38	-26.4	19.21	0.71
WMull		0.231	4.17	18.0	9.7	2.25	-27.6	20.47	0.76
Mor	*C. occidentalis*	0.097	3.79	39.2	10.1	0.98	-31.3	24.36	0.90
MMor		0.098	6.00	35.5	13.6	1.33	-32.2	25.32	0.94
PMull		0.100	5.05	48.6	11.1	1.11	-28.9	21.83	0.81
WMull		0.097	6.31	65.0	10.3	1.00	-31.9	25.00	0.93
Mor	*C. havetioides*	0.336	6.56	19.7	4.8	1.61	-25.9	18.68	0.69
MMor		0.405	5.89	21.2	5.1	2.06	-28.4	21.31	0.79
PMull		0.358	5.67	15.9	5.8	2.08	-26.3	19.10	0.71
WMull		0.386	7.78	20.2	7.5	2.90	-27.4	20.26	0.75
Mor	*C. racemiflora*	0.226	8.39	37.2	7.2	1.63	-29.4	22.36	0.83
MMor		0.240	9.12	38.0	8.2	1.97	-28.0	20.88	0.77
PMull		0.192	6.29	33.3	10.3	1.97	-27.0	19.84	0.73
WMull		0.194	9.39	48.5	10.3	2.00	-28.2	21.09	0.78
Mor	*L. octandra*	0.233	4.26	18.3	9.9	2.31	-29.2	22.15	0.82
MMor		0.188	6.28	33.1	10.1	1.90	-28.9	21.83	0.81
PMull		0.159	6.57	41.0	8.6	1.37	-29.2	22.15	0.82
WMull		0.155	5.28	34.0	9.0	1.40	-26.6	19.42	0.72
Mor	*V. meridionale*	0.263	4.26	16.3	7.6	2.00	-29.9	22.88	0.85
MMor		0.280	5.23	18.9	5.9	1.65	-28.5	21.41	0.79
PMull		0.255	3.87	15.1	8.5	2.17	-28.2	21.09	0.78
WMull		0.195	4.74	24.3	8.1	1.58	-28.7	21.62	0.80

showed the largest deviation from the overall mean and median values of 0.19 and 0.21 $kg\,m^{-2}$. Being the only deciduous species of the seven and shedding most of its leaves in January and February [*Tanner*, 1980a], the presently found low LMA values for *Clethra occidentalis* are probably affected by the date of sampling (19–27 March 1996).

Rates of dark respiration did not mirror the rates for maximum assimilation A^a_{max}. Respiration rates were rather uniform: averages ranged between -0.72 $\mu mol\,m^{-2}\,s^{-1}$ for *Clethra occidentalis* to -1.13 $\mu mol\,m^{-2}\,s^{-1}$ for *Alchornea*

Table 6.4: Average values for leaf mass per unit area (LMA), maximum assimilation per unit leaf area (A^a_{max}, $\mu mol\,CO_2\,m^{-2}\,s^{-1}$) and per unit leaf mass (A^m_{max}, $\mu\,mol\,CO_2$ - $kg^{-1}\,s^{-1}$), rates of dark respiration ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$), total nitrogen concentration per unit leaf mass ($mg\,g^{-1}$) and area ($g\,m^{-2}$), isotope composition and stomatal traits for four forest types (densities n and length of guard cells L and hypothetical minimum stomatal resistance r^{min}_{sto}). Averages and standard deviations (std.) have been weighted for the basal area distribution of the seven principal species (Table 6.3).

Forest	LMA	A^a_{max}	A^m_{max}	R_d	N	N	δ^{13}C	n	L	r^{min}_{sto}
	$kg\,m^{-2}$				$mg\,g^{-1}$	$g\,m^{-2}$	[-]	mm^{-2}	μm	$s\,m^{-1}$
Mor	0.24	5.42	23.6	-0.84	9.3	2.15	-28.9	283	12.3	25.0
std.	0.05	1.45	7.6	0.17	2.5	0.43	1.3	92	5.5	8.0
MMor	0.22	6.69	31.4	-0.79	9.3	1.93	-28.7	30	9.5	30.2
std.	0.06	1.53	7.2	0.15	1.8	0.25	1.0	95	4.0	4.8
PMull	0.18	5.40	31.7	-0.89	11.1	2.0	-27.2	234	13.0	28.5
std.	0.04	1.17	10.6	0.17	2.4	0.5	1.2	70	4.3	5.3
WMull	0.16	7.31	49.9	-0.84	10.3	1.6	-29.2	212	15.0	27.3
std.	0.05	1.84	14.4	0.17	0.8	0.7	2.0	92	5.7	8.2

Table 6.5: Average rates of dark respiration R_d ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$) and their standard deviations (n = 12–30) for seven principal tree species.

Species	*A.lat*	*C.glo*	*C.occ*	*C.hav*	*C.rac*	*L.oct*	*V.mer*
avg.	-1.13	-0.79	-0.72	-1.03	-0.96	-0.74	-0.37
s.d.	0.29	0.17	0.31	0.34	0.34	0.14	0.17

latifolia, except for *Vaccinium meridionale* which showed a low respiration rate at $-0.37\ \mu mol\,m^{-2}\,s^{-1}$ (Table 6.5).

6.3.2 Foliar nitrogen concentrations and carbon isotope composition

In partial contrast to what was found for the carbon assimilation rates of the respective species (no evidence for reduced values in the more stunted forest types) foliar nitrogen concentrations in *Vaccinium meridionale* and *Cyrilla racemiflora*, and in particularly in *Clusia* cf. *havetioides* and *Chaetocarpus globosus*, seemed to be lower (but not significantly so) in the Mor and MMor forests. Although comparisons are hampered somewhat by the lack of replications, concentrations in the leaves of the latter two species showed a reduction of 30 % compared to Mull-type foliage. Also, concentrations of N in *Clusia* cf. *havetioides* and *Vaccinium meridionale* (5.1–8.5 $mg\,g^{-1}$) were significantly lower compared to these in the other species (regardless of forest type) whereas nitrogen concentrations in *Alchornea latifolia* leaves were quite high (12.3–15.3 $mg\,g^{-1}$; Table 6.3). When converted to amounts of nitrogen per unit leaf area, contrasts in nitrogen concentrations between species were reduced and nitrogen was in fact found to be higher in at least one of the Mor-type forests for three out of seven species.

Table 6.6: Density n, length of opening along the longest axis L, tube depth l, estimated pore diameter d, and the calculated minimum resistance to the diffusion of water vapour r_{sto}^{min} [*Monteith and Unsworth*, 1990] of stomata observed at the bottom side of leaves of seven principal tree species in the Mor, MMor, PMull, and WMull forest types.

Forest	Species	n $[mm^{-2}]$	L	l[1] $[\mu m]$	d	r_{sto}^{min} $[s\,m^{-1}]$
Mor	*A. latifolia*	145	18.3	8.60	12.94	25.2
MMor		145	19.1	-	13.51	28.6
PMull		150	18.6	-	13.15	28.6
WMull		165	16.3	-	11.53	32.4
Mor-	*C. globosus*	349	12.7	6.02	8.98	18.2
MMor		237	11.8	-	8.34	30.7
PMull		278	9.8	-	6.93	35.5
WMull		304	9.0	-	6.36	37.7
-	*C. occidentalis* [1]	98	20.6	5.2	14.57	28.4
Mor	*C. havetioides*	143	22.2	5.16	15.70	17.4
MMor		140	19.5	-	13.79	21.4
PMull		141	18.1	-	12.80	23.9
WMull		126	20.6	-	14.57	21.9
Mor	*C. racemiflora*	245	14.7	5.16	10.39	18.8
MMor		239	10.0	-	7.07	36.0
PMull		302	11.6	-	8.20	22.3
WMull		293	13.0	-	9.19	19.1
Mor	*L. octandra*	356	6.8	2.58	4.81	29.3
MMor		392	6.8	-	4.81	26.7
PMull		251	8.8	-	6.22	27.8
WMull		277	7.9	-	5.59	30.0
Mor	*V. meridionale*	316	6.3	5.16	4.45	60.0
MMor		331	7.8	-	5.52	39.1
PMull		244	8.6	-	6.08	45.4
WMull		310	6.6	-	4.67	56.2

[1] no data available; values taken from *Tanner and Kapos* [1982].

At 1.0–1.3 $g\,m^{-2}$, nitrogen concentrations on a leaf area basis in *Clethra occidentalis* were 50 % below those for the other species (overall mean and median concentration: 2.1 $g\,m^{-2}$). However, this is rather the result of the low LMA values derived for *Clethra occidentalis* than because of inherently low nitrogen concentrations (Table 6.3). Average foliar nitrogen concentrations per forest type did not show a positive trend with forest stature when expressed on a mass basis but there is an inverse trend with canopy height for nitrogen per unit leaf area because of the definite increase in LMA in the Mor-type forests (Table 6.4).

Because the majority of leaf nitrogen is bound in photosynthetic enzymes,

Table 6.7: Results of rank-sum-maximum tests for dominance [*Sachs*, 1970] for foliar characteristics of seven principal tree species. The species with the statistically highest and lowest values for the parameters listed in Tables 6.3 and 6.6 are given for a significance levels $\alpha = 0.05$ (*) or $\alpha = 0.01$ (**). NSD: no significant dominant species.

Variable†	SLA	A^a_{max}	A^m_{max}	N [%]	N $[g\,m^{-2}]$	δ^{13} C
maximum	*C. occ.***	*C. rac.***	*C. occ**.	*A.lat.***	*C.glo.**	NSD
minimum	*C. hav.***	*C. glo.**	NSD	*C. hav.***	*C. occ.***	*C. occ.**

Variable†	a	L	r^{min}_{sto}
maximum	NSD	*C. hav.**	*V. mer.**
minimum	*C.hav.***	NSD	*C. hav.**

†parameter units given in Table 6.3 and Table 6.6.

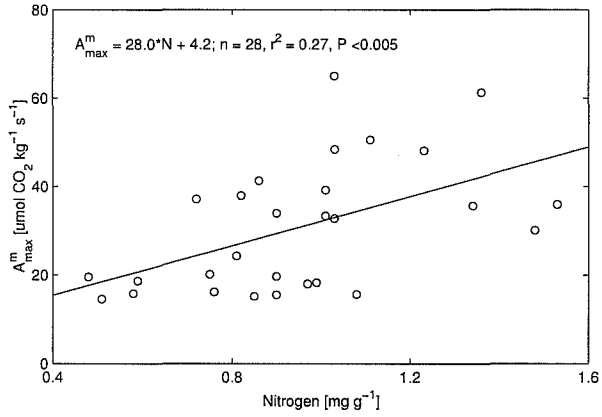

Figure 6.1: Relationship between nitrogen concentrations and maximum carbon assimilation rates (A^m_{max}) per unit leaf mass for leaf discs of seven principal species in the Mor, MMor, PMull, and WMull forests.

a strong correlation is expected between photosynthetic capacity and leaf nitrogen concentration [*Mulkey et al.*, 1996; *Sparks and Ehleringer*, 1997]. Also, considering the positive interaction between A_{max} and daytime net carbon gains [*Zotz and Winter*, 1993], the correlation between N concentration and A_{max} is expected to be positive. However, no such relationship emerged from the present data, be it at the individual species level or at the plot level. However, treating each species in each plot as an individual reading resulted in a weak ($r^2 = 0.27$; $n = 28$) but significant positive relationship between nitrogen per unit mass and A^m_{max} (P< 0.005; Fig. 6.1). When the values of A^m_{max} were subjected to a log-transformation, the r^2 increased to 0.30.

Values for ^{13}C composition ranged between -26.0 and -32.2, but variability was generally small, both between forest types or individual species and between species (Table 6.3). As a result, the overall mean and median values

hardly differed, being −28.3 and −28.2, respectively. Values of discrimination against ^{13}C (Δ) and p_i/p_a varied between 18.79 and 25.32 and 0.70 and 0.94, respectively (Table 6.3). Although three out of seven species showed the highest discrimination against ^{13}C in the Mor-type forests, no consistent patterns that followed forest physiognomic trends were evident. The highest Δ value was found for *Clethra occidentalis* which also exhibited the lowest nitrogen concentrations (Table 6.3).

6.3.3 Stomatal characteristics

None of the species had stomata on the upper surface of the leaf laminae. Significant differences were obtained between species for stomatal density and the length of the stomatal opening (guard cell length) but, once again, contrasts observed between sites were neither consistent nor significant. Plot-averaged stomatal densities were lower in the Mull-type forests compared to Mor-type forests, although the standard deviations were large (Table 6.4). *Alchornea latifolia* and *Cyrilla racemiflora* showed the highest stomatal densities in the taller-statured forest, whereas *Clusia* cf. *havetioides* and *Lyonia* cf. *octandra* exhibited an opposite pattern (Table 6.6). A significant negative correlation was obtained between stomatal density and mean length of the stomatal opening (guard cell length) after bulking all species and plots ($r^2 = 0.79$, $n = 25$, P< 0.0001).

'Minimum' stomatal resistances (r_{sto}^{min}) were calculated using the somewhat simplistic method of *Monteith and Unsworth* [1990] (Eq. 6.2) in an attempt to capture variations in stomatal densities and dimensions in a single functional parameter. The tentative increase in leaf thickness in the WMull–Mor sequence, and thus the stomatal tube length (l), could not be taken into account because l was not determined (Table 6.6). However, taking the results at face value, r_{sto}^{min} was found to vary considerably between species. Regardless of forest type, the highest values were obtained for *Vaccinium meridionale* and the lowest for *Clusia* cf. *havetioides*, with an overall average and median value of 30 $s\,m^{-1}$ and 27 $s\,m^{-1}$. No trend with forest stature was found for plot-based averages of r_{sto}^{min}, presumably because of the opposite trends derived for stomatal opening and stomatal density (Table 6.4).

6.4 Discussion

6.4.1 Photosynthetic capacity

Although measurements of A_{max} were carried out on cut branches rather than on undisturbed tree leaves, no major disturbance to the photosynthetic apparatus is expected. All branches were of considerable size, with the water columns in the xylem vessels maintained, while measurements were completed within 30 minutes after sampling. *Aylett* [1985] reported that rates of net photosynthesis on cut shoots of *Clethra occidentalis* and *Cyrilla racemiflora* were not reduced significantly before 2 and 6 days after collection, respectively. On the other hand, based on changes in stomatal conductance, *Aylett* [1985] concluded

that measurements on cut branches could lead to substantial underestimation of photosynthetic rates. However, considering the much shorter time span involved in the present study (where, in addition, branches remained at the site of collection), the effects on A_{max} are probably small.

One could argue that the instantaneous maximum rates of carbon assimilation are not representative of the integrated daytime light conditions normally experienced by the montane forests given the expected attenuation of photon flux density by low cloud. However, a strong relationship between instantaneous A_{max} and integrated daytime net carbon gain has been reported by *Zotz and Winter* [1993]. In combination with the finding that the photosynthetic capacity of leaves depends on the light regime under which they have developed [*Field*, 1988] this suggests that A_{max} may give a good indication of integrated, long-term, CO_2 assimilation.

At 5.7 $\mu mol\, m^{-2}\, s^{-1}$ the median value ($n = 28$) of A^a_{max} is at the low end of the reported range for tropical tree species (5–25 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$; *Vitousek et al.* [1990], *Meinzer et al.* [1992], *Zotz and Winter* [1993], *Hogan et al.* [1995], *Mulkey et al.* [1996]). However, the present results fall within the typical range of 4–8 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ for primary/non-pioneer tree species in tropical lowland areas [*Hogan et al.*, 1995; *Bruijnzeel and Veneklaas*, 1998] and are only slightly below the mean maximum rate of 9.3 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ reported for a variety of trees growing under perhumid conditions on poor soils in the Amazonian basin [*Reich et al.*, 1991]. The present values are also very similar to the maximum rates of 4–7 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ reported by *Aylett* [1985] for *Clethra occidentalis* and *Cyrilla racemiflora* trees growing close to the WMull plot. Our values of A^a_{max} for *Cyrilla racemiflora* (6.3–9.4 $\mu mol\, CO_2$-$m^{-2}\, s^{-1}$), however, are well above the rates reported for this species by *Aylett* [1985] (*c.* 4 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$). In further contrast to the findings of *Aylett* [1985], the present data show that average net photosynthesis at leaf level, and therefore the efficiency with which intercepted light can be utilized (at least at the top of the canopy), is not particularly low in any of the forest sites compared to primary lowland forest [*cf. Bruijnzeel and Veneklaas*, 1998].

6.4.2 Foliar nitrogen concentrations and carbon isotope composition

With a mean concentration of N of less than 1.0 % dry weight, the current values are at the low end of the range reported for other mountains in the wet tropics (0.8–2.2 %, *Tanner et al.* [1998]). The presently found nitrogen concentrations, the absence of any consistent inter-site differences for individual species and the deviating values for *Vaccinium meridionale* and *Clethra occidentalis* agree with those previously established for the Mor and Mull forests [*Tanner*, 1977a]. Plot-average nitrogen concentrations (by weight) were lower in the Mor-type forests but higher when expressed on an areal basis (Table 6.4).

Foliar δ^{13} C values have been related to a spectrum of (a)biotic factors that influence leaf gas exchange capacity [*Körner et al.*, 1988; *Ehleringer and Cooper*, 1988; *Farquhar et al.*, 1989; *Meinzer et al.*, 1992; *Ehleringer et al.*, 1993]. Gener-

ally, these studies were conducted along elevational gradients covering a range of environmental conditions [*cf. Vitousek et al.*, 1990; *Meinzer et al.*, 1992; *Sparks and Ehleringer*, 1997]. In the present case, altitudinal differences between forest types are small or negligible (*cf.* Fig. 2.1) and climatic conditions (especially radiation patterns) can be considered to be similar for all forest plots. The present values of δ^{13} C (-26.0 to -32.2; Table 6.3) span the reported range for low altitude herbaceous plants in non-water stressed, sunlit locations in the tropics (-28.1 to -30.78; *Körner et al.* [1991]) but they are mostly lower (more negative) than the range of -29.4 to -24.0 reported for leaves of *Metrosideros polymorpha* on Hawaii [*Vitousek et al.*, 1990; *Meinzer et al.*, 1992; *Kitayama et al.*, 1998]. As was also the case for values of A_{max} (Section 6.3.1), δ^{13} C values for the upper canopy leaves in Amazonian lowland rain forests on highly depleted soils (-28.7 to -30.5) were very similar to the presently found results [*Medina and Minchin*, 1980]. Sun-exposed leaves in tall lower montane forest in the Luquillo Mountains, Puerto Rico showed δ^{13} C values between -27.59 and -30.09 [*Medina et al.*, 1991], compared to -29.8 for dwarf forest on poorly drained soils in the same area [*Fischer and Tieszen*, 1995]. In the latter study, however, sampling was not restricted to sunlit leaves in the top of the canopy.

The lack of contrasts in δ^{13} C values between lowland Amazonia and the montane Caribbean sites (Jamaica, Puerto Rico) suggests that the effect of a lower atmospheric humidity deficit brought about by the presence of fog and low cloud in montane areas is small. Theoretically, discrimination against δ^{13} C increases under low *VPD* because of the associated reduction in stomatal response. Also, the diffusive capacity of the leaves will be hampered upon wetting by fog (which wets the whole leaf surface rather than only the top side as rainfall is supposed to do). This causes p_i/p_a and Δ to decrease and δ^{13} C to increase (*i.e.* become less negative) [*Sparks and Ehleringer*, 1997]. However, no such pattern emerges from the present data (Table 6.3).

Soil water stress may influence stomatal behaviour in a similar way as high atmospheric vapour deficits do [*Monteith and Unsworth*, 1990]. Stomatal closure will reduce both the stomatal conductance and p_i/p_a, the effect of which will be expressed, again, as a reduction in Δ (or increased, less negative δ^{13} C). It was suggested in Section 5.5.4 that the more shallow-rooted Mor-type forests with their shallower soils may be slightly more sensitive to prolonged droughts (which are rare but may occur in the study area) than the Mull forests growing on deeper clay soils. However, the absence of any consistent inter-site differences in isotope composition between forest types (Table 6.4) suggests that differences in soil moisture availability are not of crucial importance.

Finally, the structure of a canopy may also influence the vertical distribution of δ^{13} C values in the canopy. This is because CO_2 produced by litter decomposition and root respiration tends to be ^{13}C-depleted relative to the average atmospheric CO_2 [*Medina et al.*, 1991; *Ducatti et al.*, 1991; *Fischer and Tieszen*, 1995]. Enhanced ventilation in shorter-statured forests with more open canopies (and therefore less negative δ^{13} C) was proposed by *Fischer and Tieszen* [1995] as an explanation of the observed contrasts in δ^{13} C values between 20–30 m tall forests and 2–3 m stunted montane forest in Puerto Rico (-30.7 *vs.* -29.8).

The average δ^{13} C values for the different forest types of the study area (Table 6.4) do not support such an explanation. Not only do the values for the taller-statured PMull and WMull forest span the narrow range for the shorter-statured and better ventilated (because of their lower LAI and better exposure; *cf.* Table 6.1) Mor and MMor forests (Table 6.4), but they also do not reflect the differences in decomposition and root respiration rates between the two forest types (both lower in the MMor compared to the PMull forest; Sections 9.3.1 and 9.3.4).

6.4.3 Stomatal characteristics

The presently found negative correlation between stomatal density and the length of the stomatal opening (guard cell length; Section 6.3.3) confirms the previous findings of *Tanner and Kapos* [1982] for the Mor and Mull forest of the study area. A similar result has been reported for warm temperate rain forest in Japan [*Grubb et al.*, 1975].

Not surprisingly, our estimates of r_{sto}^{min} are much lower than the average resistance reported for tropical rain forest (*c.* 160 $s\,m^{-1}$; *Körner* [1994], *Kelliher et al.* [1995]) because only stomatal dimensions (but not behaviour) were taken into consideration in the present calculations. The present underestimation of r_s based on stomatal traits (Eq. 6.2) may also partly be the result of interference between individual pores as diffusion shells tend to overlap at high densities [*Monteith and Unsworth*, 1990]. Our values are also much lower than those suggested by the porometer measurements of *Kapos and Tanner* [1985] in the vicinity of the WMull and Mor sites. They reported a minimum value of 800 $s\,m^{-1}$ for leaves of *Cyrilla racemiflora*. Porometric measurements on the same principal tree species as the ones included in the photosynthesis experiment were also performed in the low regenerating vegetation at Bellevue Peak during conditions with *PPFD*>1000 $\mu mol\,m^{-2}\,s^{-1}$ and a relative humidity of *c.* 80% using an automatic diffusion porometer (*Delta-T Mark III*). An average r_s of *c.* 350 $s\,m^{-1}$ was obtained, with values ranging between 190 $s\,m^{-1}$ for *Vaccinium meridionale* to 630 $s\,m^{-1}$ for *Podocarpus urbanii* (Podocarpaceae), a conifer species that primarily occurs in Mull-type forests [*Tanner*, 1977a, *cf.* Table 2.2].

6.4.4 Forest stature and tree physiological characteristics

Neither potential photosynthetic capacity, stomatal behaviour (r_{sto}^{min}), dimensions and density for individual species nor isotopic composition appear to be consistently higher in the taller-statured Mull forests compared to the lower-statured Mor varieties (Table 6.3). At the stand (plot) level, however, the trend for maximum carbon assimilation rates per unit leaf mass (A_{max}^{m}) parallels that for forest stature (Table 6.4). Also, foliar concentrations of nitrogen in Mull-type forests were higher than in Mor-type forests (Table 6.4), which may be indicative of enhanced (maximum) photosynthetic capacity [*Zotz and Winter*, 1993; *Mulkey et al.*, 1996; *Sparks and Ehleringer*, 1997].

A stand's productive capacity depends also on the total photosynthetic photon flux density (*PPFD*) that is absorbed by the leaves at all canopy levels, *i.e.* on forest LAI. Although solar radiation in the study area is reduced by about 16 % compared to the lowlands [*Aylett*, 1985], *PPFD* levels in 1995 fell below the 500 $\mu mol\, m^{-2}\, s^{-1}$ threshold for light-saturated photosynthesis for only about 20 % of the time that light conditions were potentially non-limiting (generally between 07:30 and 17:10 h; Section 4.4.3). As such, *PPFD* levels in the study area must be considered adequate (as well as comparable for the different forest types) and differences in carbon gain between forests can be expected to primarily reflect differences in LAI (Table 6.1). A first approximation of the gross carbon gains (*i.e.*, the product of A^a_{max} and LAI for the 9.5 h period of sufficient light between 07:30 and 17:00 h), suggests maximum annual gross carbon assimilation totals of 3.3, 4.1, 4.0, and 5.6 $kg\, C\, m^{-2}\, yr^{-1}$ for the Mor, MMor, PMull, and WMull, respectively. Repeating these exercise for the rates of dark respiration (Table 6.4) during the 14.5 h that light levels were not sufficient gives the following respiration losses: -0.79, -0.73, -1.02, and -0.98 $kg\, C\, m^{-2}\, yr^{-1}$ for the Mor, MMor, PMull, and WMull, respectively. Taken together, the respective approximate net annual carbon gains would be: 2.5, 3.4, 3.0, and 4.6 $kg\, C\, m^{-2}\, yr^{-1}$. Because these calculations are extremely simplified (contrasts in light extinction throughout the forest canopies, for example, were not taken into consideration), the resulting absolute values are approximate at best. However, on a relative scale, the highest and lowest values are clearly associated with the tallest (WMull) and shortest (Mor) forest, respectively. Although intermediate values were derived for the intermediately-statured PMull and MMor forests, their ranking does not parallel that for canopy height. The above contrasts in annual carbon gain between the WMull and Mor forests are mirrored by their relative annual wood production rates, which were estimated at *c.* 1.0 $t\, ha^{-1}$ and 0.5 $t\, ha^{-1}$, respectively [*Tanner*, 1980b]. Needless to say, differences in net productivity and wood increment can only explain a reduction in forest stature if the forests of interest have similar life spans.

Summarizing, it may be concluded that forest stature in the study area is not caused by photosynthetic capacity at the leaf level as there is no evidence that the photosynthetic apparatus is significantly different in any of the sites. Contrasts between individual species, however, are well-established (Table 6.3), making species distribution an important factor in the determination of stand functioning (Table 6.4).

As such, it is possible that the environmental influence on foliar characteristics of a certain species induced by plot location is much less (if existing at all) than intrinsic variations between species themselves. Furthermore, although direct evidence is lacking, the distribution of the respective species may well depend on their capacity to adapt to (or their sensitivity to) the characteristic environmental situation in a given site. In view of the overall lack of differences in photosynthetic capacity at the leaf level between the studied forest types, but given the abnormal physiognomy of the vegetation of the Mor and MMor forests (*i.e.* gnarled appearance and multiple stem development), it is believed that edaphic conditions, and especially the development of acid

Mor humus, constitute a key factor. The soils of the studied forests are poor, but nutrient uptake in the most stunted forests seems especially reduced due to high acidity and consequently high levels of potentially toxic 'free' aluminium (Fig. 2.9). In contrast to the Mull situation, root distribution in the Mor forest is concentrated in the accumulated humus layer and the frequent occurrence of leaning stems in the Mor forest [*Tanner*, 1977a] may be caused by a lack of adequate anchoring. Finally, the adverse soil conditions in the Mor and MMor forests may well increase the maintenance cost for the below-ground biomass as root damage due to toxic aluminium levels is likely to occur and high root turnover rates are expected. High below-ground carbon demands rather than low production potential *per se* are therefore believed to be responsible for the reduction in stem growth [*cf. Bruijnzeel and Veneklaas*, 1998].

7

NUTRIENT DYNAMICS IN TWO UPPER MONTANE RAIN FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA. I. NUTRIENT FLUXES IN WATER*

ABSTRACT

To quantify the nutrient fluxes in water in two upper montane forests of contrasting stature at c. 1820 m a.s.l. in the Blue Mountains, Jamaica, the chemical composition of rainfall, cloud water, net precipitation (throughfall and stemflow), litter percolate, topsoil water and drainage was determined. Annual inputs of nutrients in bulk precipitation varied from less than 0.13 kg ha^{-1} for PO_4-P to 35.9 kg ha^{-1} for Cl. Inputs showed a distinct seasonal variation in agreement with the distribution of rainfall. Nutrient inputs via cloud water ranged between 3% (K and NH_4-N) and 14 % (Mg, NO_3-N) of the corresponding annual accession via bulk precipitation in the taller-statured but sheltered PMull forest and between 7 and 35 % in the shorter-statured but exposed MMor forest. Overall nutrient accession to the forest floor via net precipitation in the MMor forest was typically 25–30 % lower (K, Na, Cl, NH_4-N) or similar (Ca, Mg, PO_4-P and NO_3-N) to that in the PMull forest. Significant amounts of NO_3-N were retained in the canopies of both forests. Amounts of nutrients carried in litter percolate (i.e. readily available to plants) in the MMor forest were typically 45–75 % of those in the PMull but PO_4-P was c. 20 % higher. In the PMull forest, the amounts of nutrients leaving the soil profile via drainage generally constituted only a small fraction of the corresponding fluxes in litter percolate: 8–12 % (K, Ca), 26–29 % (NH_4-N, Mg, N_{tot}) and 44 % for PO_4-P. Nitrate showed a net loss of 1.2 kg ha^{-1} yr^{-1} from the soil but NH_4-N and N_{tot} accumulated (at rates of 4.3 and 20 kg ha^{-1} yr^{-1}). Trends for the MMor forest were largely similar, although net losses of Si and NO_3-N were higher (46 and 7 kg ha^{-1} yr^{-1}) than in the PMull (19 and 1.2 kg ha^{-1} yr^{-1}), the degree of retention for base cations, Cl, SO_4-S, N_{tot}, and NH_4-N was smaller (32 to 1.3 kg ha^{-1} yr^{-1}).

For the tall-statured PMull forest, the net ecosystem nutrient balance (inputs via P+CW minus losses via drainage) were negative for Al, Mg, N_{tot}, Na, and Si (losses

*With: L. A. Bruijnzeel. A slightly modified version of this chapter (Part I in a series of three) will be submitted to the *Journal of Ecology*.

2–27 $kg\,ha^{-1}\,yr^{-1}$); NO_3-N was lost at a rate of <4 $kg\,ha^{-1}\,yr^{-1}$; losses of K and total P were small (<1 $kg\,ha^{-1}$); PO_4-P, Ca and NH_4-N accumulated in the ecosystem (0.1–2.5 $kg\,ha^{-1}\,yr^{-1}$). Net annual losses of Na, Mg, and NO_3-N from the MMor forest (3–6 $kg\,ha^{-1}$) were smaller than from the PMull; PO_4-P, K, NH_4-N, Ca, and Cl accumulated (0.1–9 $kg\,ha^{-1}$). The annual ecosystem losses of SO_4-S, Al and Si from the MMor (5, 6 and 50 $kg\,ha^{-1}$) were increased compared to those from the PMull. Overall, net losses of key nutrients appeared to be smaller for the lower-statured MMor forest. The amounts of Ca, Mg, and K added annually to the soil via litter percolate largely exceed the corresponding requirements for gross uptake (estimated as the nutrient requirements for annual litterfall production and stem increment) in both forests; the requirements for P and N exceed the annual additions via LP roughly by a factor two. The difference between the two forests are slight and thus cannot be held responsible for their contrast in stature.

7.1 INTRODUCTION

The comparison of site conditions and ecological processes in short- and tall-statured tropical montane forests to evaluate the cause(s) of forest stunting is usually hampered by the fact that forests of contrasting stature along an elevational gradient are not only subject to corresponding changes in soil type and climatic conditions but generally also differ floristically [*Proctor et al.*, 1988, 1989; *Grieve et al.*, 1990; *Veneklaas*, 1990; *Pendry and Proctor*, 1996b, a; *Liebermann et al.*, 1996]. A striking example of forests of contrasting stature but with similar species assemblages that experience similar climatic- but contrasting edaphic conditions, is found in the Blue Mountains of Jamaica between *c.* 1600 and 1800 *m* a.s.l. along a ridge between John Crow Peak and Sir John Peak [*Grubb and Tanner*, 1976; *Tanner*, 1977a, b, ; Chapter 2]. *Shreve* [1914] ascribed the contrasts in stature between tall ravine forest, intermediate-statured forest on windward slopes and the short-statured, stunted forest on ridge tops in the area largely to differences in atmospheric humidity (notably the exposure to fog) whereas *Tanner* [1977a, 1985] and *Healey* [1990] emphasized contrasts in soil fertility. *Bruijnzeel* [1989a] drew attention to the fact that the annual inputs of nutrients to Jamaica's montane forests via bulk precipitation [*Tanner*, 1977b] greatly exceeded the amounts incorporated annually as trunk biomass [*Tanner*, 1985], suggesting that either the nutrients become immobilized upon entering the soil or that the trees are unable to make optimum use of them [*cf. Bruijnzeel et al.*, 1993]. *Tanner et al.* [1998], on the other hand, suggested that nutrient concentrations in precipitation are too low to be readily taken up by plants. However, elemental concentrations in throughfall (crown drip), stemflow, litter percolate and topsoil water (where most of the nutrient uptake takes place) are generally much higher than in above-canopy rainfall [*Steinhardt*, 1979; *Burghouts*, 1993; *Bruijnzeel et al.*, 1993].

To examine the issue further, a study of the water and nutrient dynamics of two nearly adjacent upper montane forests of contrasting stature at 1810–1825 *m* a.s.l. in the Blue Mountains was initiated in late 1994. The hydrometeoro-

logical conditions and water balances of the two forests have been discussed in Chapters 4 and 5 whereas differences in photosynthetic capacity have been dealt with in Chapter 6. The aim of this chapter is to report on the hydrochemical budgets of tall (Mull) forest and stunted (Mor) forest as a supplement to the data on soil nutrient status given by *Tanner* [1977a] and Chapter 2. Nutrient fluxes in litterfall and decomposition patterns will be discussed separately in Chapters 8 and 9, respectively.

7.2 STUDY SITES

Although developed under comparable geological and climatic conditions, montane forests above *c.* 1300 *m* elevation in the Blue Mountains may show marked contrasts in stature, soil humus type development and ecological functioning [*Tanner*, 1977a, 1980a, b, 1981]. Two forest sites of contrasting stature were selected on a SW-orientated spur (18° 05' 29" N; 76° 38' 57" W) between Sir John Peak (1900 *m* a.s.l.) and Bellevue Peak (1849 *m* a.s.l.), the distance between the latter and the sites being less than 150 *m*. The two forest sites are considered to represent intermediate stages in a sequence of forest types with increasingly acid humus and topsoil (pH 4.4 to 3.0) and a gradual reduction in forest stature from so-called well-developed 'Mull' forest (canopy height 13–17 *m*) to stunted 'Mor' forest (5–7 *m*) as identified by *Tanner* [1977a, 1980b]. The present plots are located *c.* 2 *km* East of the plots studied by *Tanner* [1977a] (see Fig. 2.1 in Chapter 2). The physiognomy, floristics, soil fauna and edaphic conditions of the respective forests have been discussed in detail in Chapter 2.

Summarizing, the shorter (main canopy height: 5–8 *m*) forest of the two was classified as 'moderately-developed' Mor forest (MMor); the taller (7–12 *m*) forest as 'poorly-developed' Mull forest (PMull). The lateral distance between the sites is <30 *m*. The MMor forest is situated on the top of the ridge (1824 *m* a.s.l.), and is more exposed to the east-southeasterly winds than the more sheltered PMull forest which is situated on a near-level slope section on the NW side of the ridge (1809 *m* a.s.l.) (Fig. 2.1). The PMull forest has a higher total basal area (BA, 53.1 m^2ha^{-1}), lower tree density (4400 ha^{-1}), less trees with multiple trunks (TWMT, 567 ha^{-1}) and a higher leaf area index (LAI, 5.0 m^2m^{-2}) compared to the MMor forest (BA 44,4 m^2ha^{-1}, tree density 6043 ha^{-1}, TWMT 1043 ha^{-1}, LAI 4.1 m^2m^{-2}).

The two forests share a number of principal tree species but the relative distribution of these species varies considerably (see Table 2.2 for details). In the PMull forest, a discontinuous litter/fermentation layer plus a thin layer of humus overlie deep clay soils (Dystric cambisol) with fresh bedrock at > 3 *m*. The shallow ($\leq$ 0.7 *m*) MMor forest soil (Folic histosol) has a thick ($\leq$ 0.5 *m*) layer of accumulated Mor humus and a well-developed surface root mat. The majority of the fine roots is observed in the top 60 and 30 *cm* below the surface in the PMull and MMor forest, respectively. Topsoil porosity is high (*c.* 80 %), decreasing to *c.* 60 % in the subsoils. Saturated hydraulic conductivity in the Ah horizon is also very high at 10.1–18.5 $m\,d^{-1}$ but decreases rapidly with depth

Table 7.1: Annual amounts (in *mm*) of rainfall (P), cloud water (CW), throughfall (Tf), stemflow (Sf), rainfall interception (E_i), transpiration (E_t), total evapotranspiration (ET), changes in soil water storage (ΔS), and drainage (D) beyond an 80 *cm* soil column in the PMull and MMor forests.

Forest	P	CW	Tf	Sf	E_i	E_t	ET	ΔS	D
PMull	3060	43	2233	399	428	620	1048	-20	2032
	% of P	1.4	73	13	14	20	34	<0.7	66
MMor	3060	104	1821	559	680	509	1189	14	1857
	% of P	3.4	60	18	22	17	39	<0.5	61

7.4 Results

7.4.1 Water balance

The components of the water budgets of the two forest plots are summarized in Table 7.1. Further details are given in Section 5.5. Rainfall at Bellevue Peak in 1995 totalled 3060 *mm*, *i.e.* 25 % above the long term (1901–1990) average rainfall at Cinchona Botanical Gardens (1500 *m* a.s.l., 3 *km* SW of Bellevue Peak; see Fig. 2.1) and 7 % above the average amount estimated for the research area (2850 *mm*, *cf.* Section 2.1.3). The volume of cloud water collected by a covered 'Grünow'-type fog gauge at Bellevue Peak (which was used for chemical analysis) amounted to 12.3 *l* or 197 *mm* (6.4 % of rainfall) when divided by the collecting surface (628 cm^2). The actual interception of cloud water by the forests was estimated at 3.4 % of total P (104 *mm*) in the MMor forest *vs.* 1.4 % of P (43 *mm*) in the PMull. Because contributions by cloud during periods with rain were not included, these figures represent underestimates (*cf.* Section 4.4.2). Volumes of throughfall (and stemflow) in the two forests were closely correlated, both amounts measured at 3–4 day intervals ($r^2 = 0.93$, $P < 0.0001$, $n = 94$) and bulked amounts ($n = 17$). Throughfall (Tf) in the PMull forest was much higher than in the MMor (73 % of P *vs.* 60 %) but this was partly compensated by the higher stemflow (Sf) fraction for the MMor (18 % of P *vs.* 13 % in the PMull) and the lower transpiration (E_t) derived for the MMor (17 % of P *vs.* 20 % in the PMull). Because overall changes in soil water storage (ΔS) were minor, the resulting amounts of drainage (D) did not differ much between the two forests (65 % and 61 % of P, respectively; Table 7.1).

7.4.2 Chemical composition of precipitation and soil water

Bulk precipitation and cloud water

The chemical composition of the sampled rain water represents both wet deposition by above-canopy rainfall as well as dry deposition of aerosols on the collecting area of the rain gauge. This is normally referred to as 'bulk precipitation' [*Whitehead and Feth*, 1964]. Because a rain gauge represents a less effective trapping surface than a forest canopy, only part of the dry deposition on the studied forests is accounted for by the bulk precipitation input [*Stoorvogel*, 1993]. Concentrations of solutes in bulk precipitation P were low compared to those in

Table 7.1: Annual amounts (in *mm*) of rainfall (P), cloud water (CW), throughfall (Tf), stemflow (Sf), rainfall interception (E_i), transpiration (E_t), total evapotranspiration (ET), changes in soil water storage (ΔS), and drainage (D) beyond an 80 *cm* soil column in the PMull and MMor forests.

Forest	P	CW	Tf	Sf	E_i	E_t	ET	ΔS	D
PMull	3060	43	2233	399	428	620	1048	-20	2032
	% of P	1.4	73	13	14	20	34	<0.7	66
MMor	3060	104	1821	559	680	509	1189	14	1857
	% of P	3.4	60	18	22	17	39	<0.5	61

7.4 Results

7.4.1 Water balance

The components of the water budgets of the two forest plots are summarized in Table 7.1. Further details are given in Section 5.5. Rainfall at Bellevue Peak in 1995 totalled 3060 *mm*, *i.e.* 25 % above the long term (1901–1990) average rainfall at Cinchona Botanical Gardens (1500 *m* a.s.l., 3 *km* SW of Bellevue Peak; see Fig. 2.1) and 7 % above the average amount estimated for the research area (2850 *mm*, *cf.* Section 2.1.3). The volume of cloud water collected by a covered 'Grünow'-type fog gauge at Bellevue Peak (which was used for chemical analysis) amounted to 12.3 *l* or 197 *mm* (6.4 % of rainfall) when divided by the collecting surface (628 cm^2). The actual interception of cloud water by the forests was estimated at 3.4 % of total P (104 *mm*) in the MMor forest *vs.* 1.4 % of P (43 *mm*) in the PMull. Because contributions by cloud during periods with rain were not included, these figures represent underestimates (*cf.* Section 4.4.2). Volumes of throughfall (and stemflow) in the two forests were closely correlated, both amounts measured at 3–4 day intervals (r^2 = 0.93, P< 0.0001, n = 94) and bulked amounts (n = 17). Throughfall (Tf) in the PMull forest was much higher than in the MMor (73 % of P *vs.* 60 %) but this was partly compensated by the higher stemflow (Sf) fraction for the MMor (18 % of P *vs.* 13 % in the PMull) and the lower transpiration (E_t) derived for the MMor (17 % of P *vs.* 20 % in the PMull). Because overall changes in soil water storage (ΔS) were minor, the resulting amounts of drainage (D) did not differ much between the two forests (65 % and 61 % of P, respectively; Table 7.1).

7.4.2 Chemical composition of precipitation and soil water

Bulk precipitation and cloud water

The chemical composition of the sampled rain water represents both wet deposition by above-canopy rainfall as well as dry deposition of aerosols on the collecting area of the rain gauge. This is normally referred to as 'bulk precipitation' [*Whitehead and Feth*, 1964]. Because a rain gauge represents a less effective trapping surface than a forest canopy, only part of the dry deposition on the studied forests is accounted for by the bulk precipitation input [*Stoorvogel*, 1993]. Concentrations of solutes in bulk precipitation P were low compared to those in

Table 7.2: Volume-weighted mean ($\overline{\alpha}$) concentrations and their standard deviations (s.d.) of hydrogen (as pH) and elemental nutrients ($mg\,l^{-1}$) in bulk precipitation (P) and cloud water (CW) at Bellevue Peak, and throughfall (Tf), stemflow (Sf), litter percolate (LP), soil water in the Ah horizon (SW), and drainage (D) for the PMull- and MMor forests. Averages for P, CW, Tf, Sf, and LP are based on 17 samples; SW and D are averages for 14 samples. Detection limits (dl., $mg\,l^{-1}$) have been added for comparison.

Element	dl.	P_{Bellevue}		CW_{Bellevue}		Tf_{PMull}		Sf_{PMull}		Tf_{MMor}		Sf_{MMor}	
		$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.
pH	-	5.52	-	5.83	-	5.90	-	5.07	-	5.95	-	5.67	-
Ca	0.05	<0.29	0.23	1.44	1.50	0.50	0.26	0.50	0.30	0.50	0.26	0.56	0.31
Mg	0.05	<0.07	0.03	0.57	0.46	0.22	0.10	0.26	0.14	0.24	0.12	0.36	0.20
K	0.05	<0.27	0.13	0.57	0.38	1.54	0.64	2.44	0.81	1.27	0.54	1.76	0.62
Na	0.05	0.67	0.30	4.15	3.35	1.09	0.39	1.35	0.70	0.91	0.32	1.19	0.52
NH_4-N	0.02	<0.13	0.09	<0.24	0.19	0.19	0.10	0.14	0.08	<0.17	0.10	0.11	0.09
NO_3-N	0.01	≪0.06	0.04	<0.46	0.62	≪0.02	0.03	≪0.056	0.072	≪0.027	0.027	≪0.046	0.10
PO_4-P	0.003	≪0.004	0.003	≪0.026	0.032	≪0.007	0.004	≪0.004	0.002	≪0.008	0.012	≪0.005	0.004
SO_4-S	0.03	≪0.13	0.10	0.78	0.55	0.45	0.30	0.79	0.38	<0.38	0.34	0.43	0.29
Cl	0.05	1.14	0.59	7.32	6.31	1.91	0.72	2.72	1.52	1.60	0.81	2.20	1.40

Element	dl.	LP_{PMull}		$SW_{\text{Ah PMull}}$		$D_{\text{Bw PMull}}$		LP_{MMor}		$SW_{\text{Ah MMor}}$		$D_{\text{BC MMor}}$	
		$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.	$\overline{\alpha}$	sd.
pH	-	5.69	-	4.77		5.07	-	5.68	-	4.10		5.06	-
Ca	0.05	2.54	0.91	0.46	0.15	0.38	0.14	1.65	0.54	0.57	0.21	≪0.11	0.10
Mg	0.05	1.10	0.44	0.54	0.07	0.42	0.08	0.93	0.43	0.84	0.20	0.41	0.12
K	0.05	4.14	1.62	0.85	0.38	0.45	0.13	2.87	1.60	0.97	0.53	0.37	0.10
Na	0.05	1.98	0.84	1.69	0.28	1.57	0.23	1.56	0.76	1.72	0.52	1.48	0.21
Al	0.05	<0.19	0.09	0.62	0.13	≪0.09	0.03	≪0.08	0.01	1.58	0.35	0.34	0.04
Fe	0.05	≪0.08	0.03	0.20	0.10	≪0.05	0.01	≪0.05	0.01	0.79	0.15	≪0.05	0.006
Si	0.05	<0.32	0.21	1.42	0.35	1.33	0.35	<0.16	1.12	2.58	1.43	2.67	0.77
NH_4-N	0.02	0.22	0.17	0.16	0.09	<0.07	0.06	0.13	0.13	0.17	0.15	<0.09	0.08
NO_3-N	0.01	<0.17	0.21	<0.16	0.16	0.27	0.23	<0.04	0.08	≪0.13	0.15	<0.16	0.20
N_{tot}	0.01	1.05	0.46	0.70	0.25	0.39	0.19	0.81	0.45	0.97	0.42	0.38	0.14
PO_4-P	0.003	≪0.006	0.012	≪0.005	0.003	≪0.004	0.003	≪0.008	0.020	≪0.004	0.004	≪0.004	0.002
P_{tot}	0.01	0.053	0.029	≪0.013	0.008	≪0.012	0.007	<0.040	0.039	≪0.028	0.030	≪0.018	0.009
SO_4-S	0.03	1.94	1.30	<0.85	0.49	≪0.34	0.16	<1.32	0.82	2.86	1.45	<0.53	0.12
Cl	0.05	4.24	2.09	2.21	0.85	2.93	0.51	2.75	1.66	3.11	1.46	1.80	0.63

The sign '<' is used whenever one of the composite samples showed a concentration below the detection limit, the sign '≪' is used whenever more than three samples had concentrations below the detection limit.

Table 7.3: The calculated contribution of maritime sources to the chemical composition of rainfall and cloud water at Bellevue Peak.

Component	Na	K	Mg	Ca	Cl	SO_4-S	NO_3-N
				$[mg\,l^{-1}]$			
Seawater†	10600	330	1500	480	18425	1102	0.002
Rainfall	0.67	0.27	0.07	0.29	1.14	0.14	0.05
Seawater component (%)	97	8	141	10	100	49	0
Cloud water	4.15	0.57	0.57	1.44	7.32	0.78	0.46
Seawater component (%)	101	23	105	13	100	56	0

†Caribbean coast, Panama [*Cavelier et al.*, 1997]

especially robust for Mg and K ($r^2 > 0.55$, P< 0.0001) and the correlation coefficients increased to $r^2 > 0.69$ after double-log transformation of the data were analyzed. No such correlations were found for NO_3-N (both sites) and for PO_4-P and NH_4-N in the MMor although both PO_4-P and NH_4-N were significantly correlated with the depth of *Tf* in the PMull forest. The negative correlations found between *Sf* volumes and log-transformed concentrations of solutes were significant for all cations and SO_4-S; no correlations were found for PO_4-P and NO_3-N. Regressions were strong for base cations (P< 0.01), particularly for K and Na in the PMull forest ($r^2 > 0.54$, P< 0.001) and for SO_4-S at both sites ($r^2 > 0.70$, P< 0.00001).

Litter percolate

Concentrations of Ca, K, Al, Fe, Cl, Si, NH_4-N in litter percolate collected in the taller-statured PMull forest were twice those found in the short-statured MMor forest (*t-test*, $n = 17$, P< 0.001). Nitrate was also distinctly higher (4 times, P< 0.0001) in the PMull whereas concentrations of Mg, Na, N_{tot}, SO_4-S and phosphorus (P_{tot} and PO_4-P) were only slightly above those short in the MMor (P< 0.05).

Compared to the corresponding concentrations in net precipitation (*i.e.* weighted means of *Tf*+*Sf*), concentrations of certain solutes increased 2–5 times (base cations, Cl) upon passage through the litter layer in the PMull forest, but only 1.5–3 times in the MMor. A minor (non-significant) drop in concentration was observed for NH_4-N in the MMor (but not in the PMull; Table 7.2). An even larger contrast between the two sites was found for NO_3-N: concentrations in PMull litter percolate were seven times those in net precipitation, whereas in the MMor forest the increase was 40 % (Table 7.2).

Soil water

Concentrations of solutes in soil water were found to decrease rapidly with time at the beginning of sampling despite the precautions outlined in Section 7.3. In some cases (K) this trend continued throughout the observation period (Fig. 7.1 and Fig. 7.2). Such patterns do not correspond with seasonal variations or other possible disturbances that might affect soil moisture chemistry. Therefore, it was

concluded that elements were initially leached from the ceramic cup samplers [*cf. Brouwer*, 1996], also because the effect was similar in the two plots (Fig. 7.1 and Fig. 7.2). Therefore, calculations of the mean nutrient concentrations in soil water (Table 7.2) and corresponding fluxes (Table 7.4) were restricted to the samples collected between April 1995 (no. 4) and January 1996 (no. 17) to avoid overestimation of the nutrient losses via drainage. Sample no. 11 for soil water in the BC-horizon of the MMor forest was also excluded from the calculations for NO_3-N (*cf.* Fig. 7.2). The averages given in Table 7.2 (using the reduced data set) are typically 20–30 % below the means that would have been obtained on the basis of all available samples. However, the contrasts would be much more pronounced for Ca and P_{tot} in water extracted from the BC horizon of the MMor (present values are 160 and 125 % lower) and for NO_3-N, Cl, and (to a lesser extent) Ca in the water from the Ah/Bw-horizons in the PMull. Average concentrations of Al and Fe were hardly affected (<10 % difference).

The strong contrast observed for the chemical composition of litter percolate in the PMull and MMor forests (generally much higher concentrations in the PMull) largely disappears when concentrations in the water extracted from the Ah-horizons are compared. In fact, concentrations of most elements in topsoil water in the PMull are (much) lower than in the MMor, indicating a reversal of the trend found for litter percolate (Table 7.2). Only NO_3-N remains slightly higher in the PMull but the difference is not statistically significant. Amounts of PO_4-P and P_{tot} in soil water were below the detection limits in more than 75 % of all soil moisture samples, rendering their mean concentrations very unreliable and most probably overestimated. In the deeper mineral soil (BC horizon in the MMor, Bw horizon in the PMull) ion concentrations in soil water are comparable for both forests (including the nitrogen species), except for Ca (PMull>MMor), Al, Si and SO_4-S (MMor>PMull) (Table 7.2).

7.4.3 Nutrient fluxes

Nutrient fluxes via bulk precipitation and cloud water

Amounts and chemical composition of bulk precipitation P (wet and dry deposition) as measured at nearby Bellevue Peak in 1995 were assumed to apply to both the PMull and MMor forests, although it is recognized that differences in aerosol trapping capacity may exist between the two forests because of differences in exposure and leaf area index. We will return to this point in the next section. Annual nutrient input via bulk precipitation varied from less than 0.13 $kg\,ha^{-1}$ for PO_4-P to 35.9 $kg\,ha^{-1}$ for Cl (Table 7.4). Inputs showed a distinct seasonal variation: generally, amounts were low during April–July and increased at the end of the summer in agreement with the distribution of rainfall (Fig. 7.3). Although solute concentrations in rainfall were generally lower during wet periods (*i.e.* most concentrations were inversely related to precipitation depth), the corresponding inputs of nutrients (including H^+) in rainfall (Fig. 7.3) were positively correlated with precipitation quantity ($r^2 > 0.30$, $P < 0.05$), except for Ca ($r^2 = 0.20$, $P > 0.05$). Robust correlations were found for Mg and K ($r^2 > 0.59$, $P < 0.0001$).

Differences in atmospheric nutrient inputs to the two study sites may further be generated by contrasts in the interception of cloud water (1.4 % in the PMull *vs.* 3.4 % in the MMor; Table 7.2). In the PMull forest, nutrient inputs by cloud water generally fell between 7 % (Ca) and 14 % (Mg, NO_3-N) of the annual nutrient accession via bulk precipitation (Table 7.4), except for K and NH_4-N (3 % each). For the more exposed MMor forest, the nutrient flux associated with fog typically ranged between 20 % (for PO_4-P, SO_4-S) and 35 % (for Mg, NO_3-N) of that in bulk precipitation. For NH_4-N and K, values were low again (7 %, Table 7.4).

Fluxes in net precipitation

In the PMull forest, the annual nutrient fluxes via net precipitation (Tf+Sf) ranged from less than 0.2 $kg\,ha^{-1}$ for PO_4-P to 53.5 $kg\,ha^{-1}$ for Cl. Between

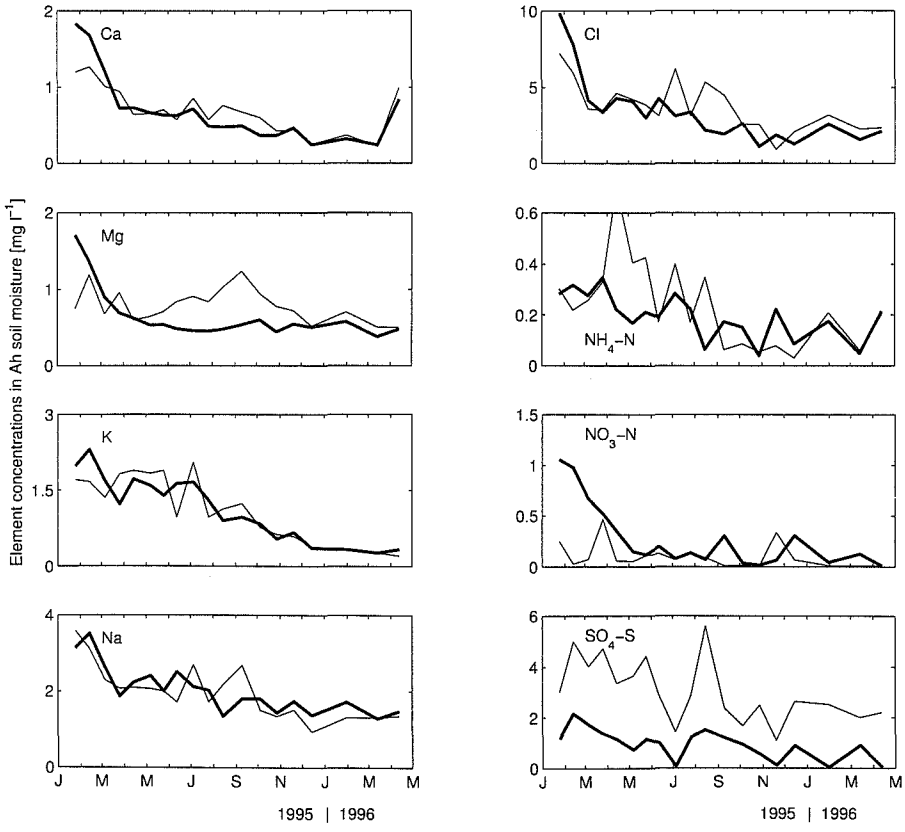

Figure 7.1: Concentrations of solutes ($mg\,l^{-1}$) in soil water samples (n = 19) extracted by ceramic-cup vacuum samplers at 3–4 week intervals between January 1995 and April 1996 from the Ah horizons in the PMull (bold line) and MMor forest (thin line).

70 % (NO_3-N) and 90 % (PO_4-P) of the nutrient transferred to the forest floor via net precipitation were contributed by *Tf* alone (Table 7.4). The relative importance of *Tf* was reduced to *c.* 70 % (ranging from 65 % for NO_3-N to 85 % for PO_4-P) in the MMor forest, in favour of contributions by stemflow (Table 7.4). Overall, nutrient additions to the forest floor via net precipitation were higher in the PMull (typically by about 25–30 % for K, Na, Cl, NH_4-N) or similar (less than 10 % difference for Ca, Mg, PO_4-P, NO_3-N).

As observed earlier for bulk precipitation (Table 7.4), solute fluxes in the precipitation components and amounts of *Tf* and *Sf* were positively correlated ($P < 0.01$, typically better correlations for *Tf*). Strong correlations ($r^2 > 0.63$, $P < 0.0001$) were found between quantities of *Tf* or *Sf* and solute fluxes of H^+ and K, (for both *Tf* and *Sf*), and for Mg, Na, and Cl (*Tf* only). The relationships were very weak and not significant ($P > 0.05$), however, for NO_3-N

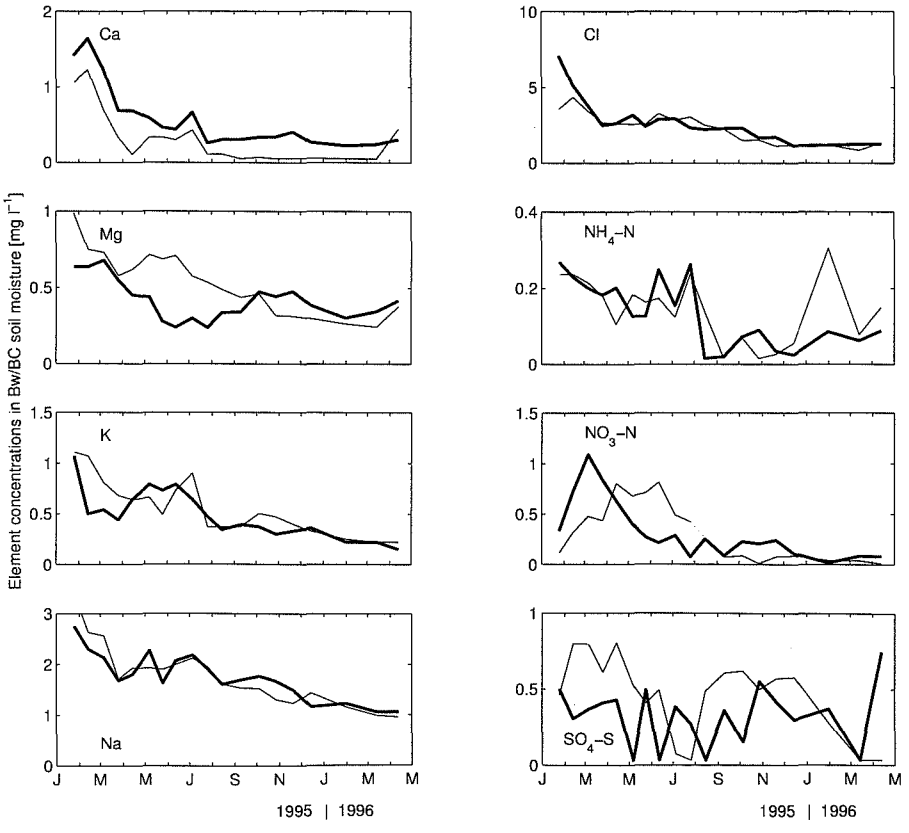

Figure 7.2: Concentrations of solutes ($mg\,l^{-1}$) in soil water samples ($n = 19$) extracted by ceramic-cup vacuum samplers at 3–4 week intervals between January 1995 and April 1996 from the Bw/BC horizons in the PMull (bold line) and MMor forest (thin line).

and *Tf* and *Sf* in the MMor (and *Tf* only in the PMull), as well as for fluxes of PO_4-P and *Tf* (both forests), SO_4-S and *Tf* in the MMor and NH_4-N and *Sf* in the MMor (*cf.* the patterns displayed in Figs. 7.4 and 7.5).

Apart from the effect imposed by rainfall interception (which renders amounts of net precipitation much smaller than incident rainfall (*cf.* Table 7.1)), contrasts in nutrient fluxes via bulk precipitation and net precipitation are caused by (1) the different efficiencies in trapping aerosols of a forest canopy and a rain gauge, and (2) leaching or retention (absorption) of nutrients by leaves and epiphyte biomass. The sum of these processes is usually referred to as net canopy leaching or retention and is evaluated by subtracting the corresponding annual inputs via *P+CW* from the respective nutrient fluxes via *Tf+Sf* [*Tukey*, 1970; *Parker*, 1983]. Net effects in the PMull forest site were mostly positive (*i.e.* leaching or deposition exceeded retention) and ranged from 0.04 $kg\,ha^{-1}\,yr^{-1}$ for PO_4-P (equal to 30 % of the annual input via *P+CW*) to 35.5 $kg\,ha^{-1}\,yr^{-1}$ for K (>400 %) (Table 7.5). About 0.7 $kg\,ha^{-1}\,yr^{-1}$ of NH_4-N

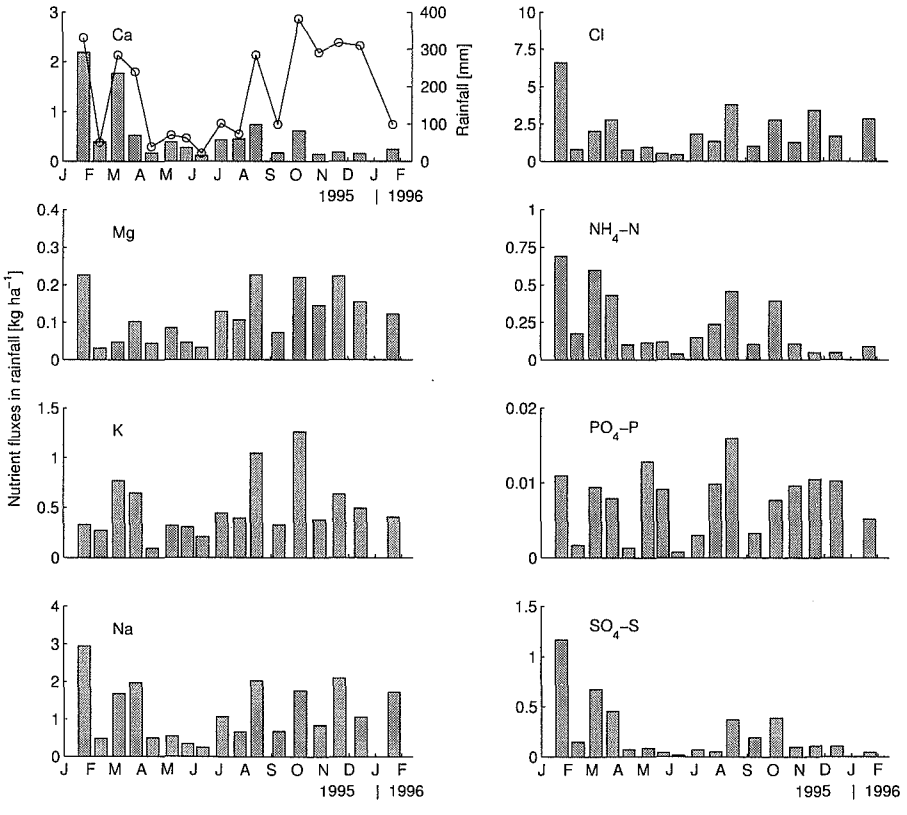

Figure 7.3: Nutrient fluxes ($kg\,ha^{-1}$) for 3–4 week periods during 1995 in bulk precipitation at Bellevue Peak (1849 *m* a.s.l.). The corresponding amounts of rainfall (circles, *mm*) have been added to the top left diagram for comparison.

appeared to be leached from the PMull canopy but a net retention was derived for NO_3-N (1.24 $kg\,ha^{-1}\,yr^{-1}$, or 65 % of the input via P+CW).

Net amounts of nutrients washed or leached from the canopy of the MMor forest were generally smaller than in the PMull (Table 7.5). This is not only due to the lower amounts of net precipitation recorded there (Table 7.1). Also, apart from the net retention derived again for NO_3-N (1.5 $kg\,ha^{-1}\,yr^{-1}$ or 67 % of the 2.24 $kg\,ha^{-1}\,yr^{-1}$ added to the forest via P+ CW), small net retention values were obtained for NH_4-N (0.4 $kg\,ha^{-1}\,yr^{-1}$) and, surprisingly, for Na (-1.8 $kg\,ha^{-1}\,yr^{-1}$). Net leaching of Cl in the MMor forest was also much smaller than in the PMull forest (2.1 *vs.* 14.8 $kg\,ha^{-1}\,yr^{-1}$; Table 7.5) whereas the concentrations of both Cl and Na in Tf and Sf were lower in the MMor as well. These results suggest that the aerosol trapping efficiency of the MMor forest is distinctly less than that of the PMull, despite the fact that the MMor is better exposed to the prevailing winds. Neither Na nor Cl are likely to be absorbed or

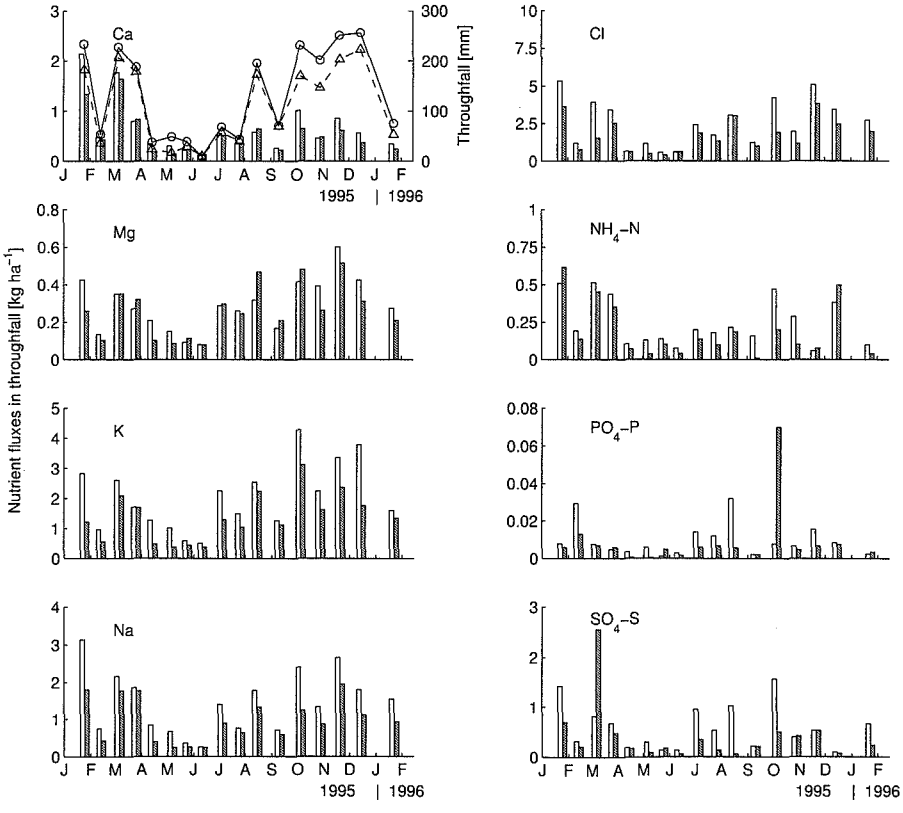

Figure 7.4: Nutrient fluxes ($kg\,ha^{-1}$) for 3–4 week periods during 1995 in throughfall for the PMull (white bars) and MMor forest (dark bars). The corresponding amounts of throughfall (mm) for the PMull forest (circles) and the MMor (triangles) have been added to the top left diagram for comparison.

leached in significant quantities [*Parker*, 1983] and it must be concluded that the apparent retention of Na by the canopy of the MMor forest is most likely caused by an underestimation of the amount of net rainfall (*cf.* Section 5.6.1).

Net canopy leaching was positively correlated with rainfall ($r^2 > 0.31$, $P < 0.05$) for the base cations and Cl in the PMull forest. The relationships for Mg and K were strongest ($r^2 > 0.54$, $P < 0.001$). For the MMor forest only Mg and K showed significant (and robust) relationships ($r^2 > 0.67$, $P < 0.0001$) but those for Ca, Na and Cl were all very poor ($P > 0.15$). Net leaching of NH_4-N, NO_3-N, PO_4-P, SO_4-S and H^+ did not show significant relationships with depth of P in either forest. Fluxes of Na, Cl, NH_4-N and PO_4-P are the same order of magnitude in $P+CW$ and $Tf+Sf$ alike. Small differences therefore (possibly as a result of measurement errors) may cause relatively large deviations from the mean net flux. However, different characteristics of the respective forest canopies may also be partly responsible.

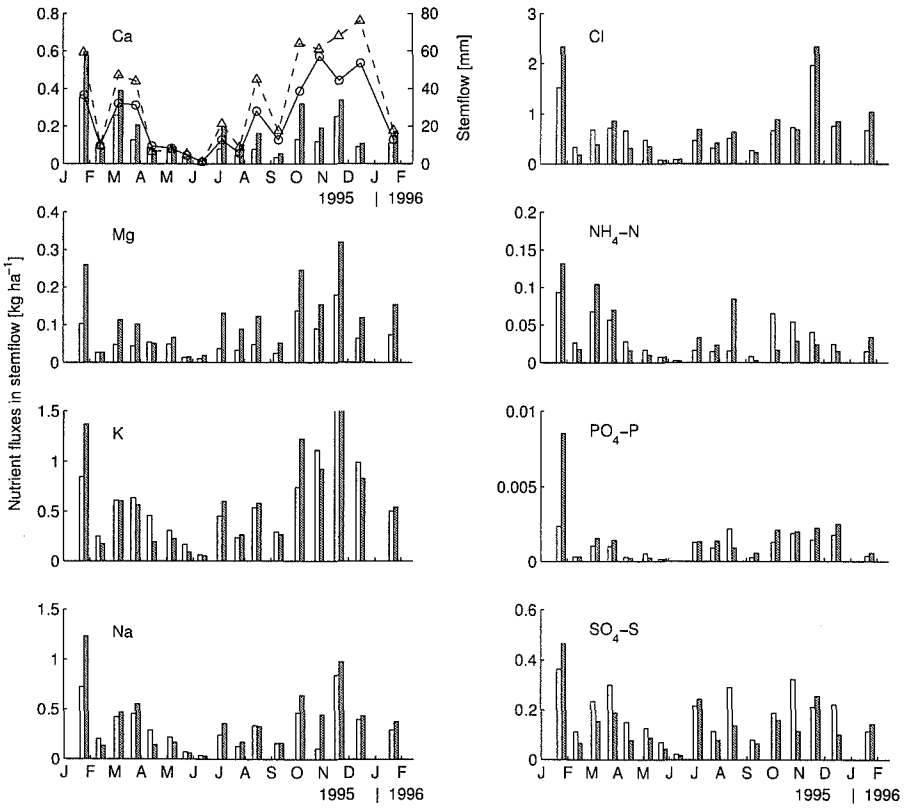

Figure 7.5: Nutrient fluxes ($kg\,ha^{-1}$) for 3–4 week periods during 1995 in stemflow for the PMull (white bars) and MMor forest (dark bars). The corresponding amounts of stemflow (mm) for the PMull (circles) and the MMor (triangles) have been added to the top left diagram for comparison.

Nutrient fluxes through the litter layer
Evaporation from the litter layer (forest floor) in the tropical rain forest is usually very small [*Jordan and Heuveldop*, 1981; *Roche*, 1982]. Therefore, and because the quantification of amounts of water percolating through the litter (*LP*) using collection plates inserted below the litter has its problems [*Burghouts*, 1993], nutrient fluxes in *LP* were simply calculated as the product of net precipitation amounts (*Tf*+*Sf*) times the nutrient concentrations in *LP* given in Table 7.2. Although the presently used concentrations may therefore be slightly elevated because of concentration by evaporation, the effect is believed to be very small. The results are listed in Table 7.4.

As shown in Table 7.4, amounts of nutrients carried in the litter percolate of the MMor forest were typically 45–75 % of those in the PMull, the chief exceptions being PO_4-P (*c.* 19 % higher in the MMor), H (8 % lower) and, particularly, NO_3-N (77 % lower). Similarly, a comparison of the nutrient fluxes in *LP* with those arriving at the forest floor in *Tf*+*Sf* (Table 7.5) shows that net increases for many elements (base cations, Al, Si, Cl, SO_4-S, as well as N_{tot} and P_{tot}) upon passage through the litter layer in the MMor were typically 40–70 % of those observed in the PMull. Once again, net leaching of NO_3-N from the litter layer in the MMor (0.3 $kg\,ha^{-1}\,yr^{-1}$) was a mere 8 % of that in the PMull (3.6 $kg\,ha^{-1}\,yr^{-1}$) whereas NH_4-N was retained (at a rate of 0.76 $kg\,ha^{-1}\,yr^{-1}$), compared to a net leaching rate in the PMull of 1.1 $kg\,ha^{-1}\,yr^{-1}$ (Table 7.5). Net leaching (MMor) or retention (PMull) of PO_4-P were small and the difference in sign of the balance between the two forests may reflect uncertainties in the measurements of *Tf* and, particularly, *Sf* rather than a real difference between sites. We will come back to these differences in net leaching of nutrients from the respective forest floors in Chapter 9 on litter decomposition.

Nutrient fluxes in the soil-complex
Comparison of the fluxes leaving the forest floor (*LP*) and the mineral topsoil (D_{Ah}) reveals a number of striking patterns, some of which differ between the two forests (Table 7.5). Large amounts of base cations (Ca, Mg, K, but not Na) are apparently taken up by the vegetation of the two plots or otherwise retained, whereas H, Al, Fe, and Si are released in large quantities, especially in the more acid MMor soil. Phosphorus (both PO_4-P and P_{tot}) are taken up or retained in small quantities by both forests but a contrasting pattern is observed for SO_4-S and the nitrogen species.

As a result of these processes, the fluxes of the respective elements passing through the Ah-horizon are much more similar between the two forests than those in the litter percolate (Table 7.4), although differences remain pronounced for H, Al, Fe, Si, and SO_4-S (all higher in the MMor) and for NO_3-N (higher in the PMull). By and large, nutrient fluxes through the subsoil were generally much smaller than in the topsoil in both forests, presumably as a result of continued uptake (plant nutrients) or complexation (Fe, Al). Once again, NO_3-N (but not NH_4-N or N_{tot}) constituted an exception in that subsoil fluxes

were either similar to those in the topsoil (MMor) or higher (PMull). Absolute amounts of Mg, K, Na, Cl and N_{tot} in subsoil drainage in the MMor forest were 75–90 % of those in the PMull, but much lower for NO_3-N (55 %) and, especially Ca (27 %). Fluxes of H, Fe, PO_4-P were all similar to those in the PMull but those of P_{tot}, SO_4-S, and Si (180 %) and Al (340 %) in particular, were distinctly higher in the MMor (Table 7.4).

Comparison of nutrient fluxes in subsoil drainage and litter percolate allows an evaluation of the overall effect of the various processes taking place in the soil (uptake, exchange, complexation, weathering, etc.). In the PMull forest, amounts of nutrients leaving the soil profile via drainage generally constituted only a small fraction of the amounts entering the mineral soil in litter percolate. Values for key nutrients ranged from 8–12 % (K, Ca), via 26–29 % (NH_4-N, Mg, N_{tot}) to 44 % for PO_4-P (Table 7.5). Overall losses of H and Si greatly exceeded inputs from litter percolate but not as much as noted earlier for the Ah-horizon. Nitrate showed a net loss of 1.2 $kg\,ha^{-1}\,yr^{-1}$ from the soil in the PMull but NH_4-N and N_{tot} accumulated at rates of 4.3 and 19.8 $kg\,ha^{-1}\,yr^{-1}$, respectively (Table 7.5). Trends for the MMor forest were largely similar, although net losses of Si (+25 %) and NO_3-N (+167 %) were higher than in the PMull whereas the degree of retention for base cations, Cl, NH_4-N, N_{tot} and SO_4-S was smaller (typically 50–70 % of values observed in the PMull). To some extent the larger net loss of NO_3-N computed for the MMor forest must reflect the underestimation of amounts brought in via net precipitation (*cf.* Section 5.6.1).

A comparison of nutrient inputs and outputs for the mineral soil thus shows a pattern of net retention and immobilization for most elements except for NO_3-N and Si (both forests) and for Al in the MMor (Table 7.5). However, the inputs of nutrients to the mineral soil via *LP* include the effects of such intra-system processes as litter production, decomposition and canopy leaching. To evaluate to what extent these forests are gaining or losing nutrients, the losses via subsoil drainage have been compared with inputs via bulk rainfall and cloud water deposition (*P*+*CW*) in Table 7.5. For the tall-statured PMull forest, the largest net losses were observed for Si, Na, N_{tot} and Mg (>6 $kg\,ha^{-1}\,yr^{-1}$) whereas NO_3-N was lost at a rate of 3.6 $kg\,ha^{-1}\,yr^{-1}$. Losses of K and total P were small whereas PO_4-P, Ca, NH_4-N accumulated in the ecosystem (Table 7.5). With the exception of net ecosystem losses of Si, Al and SO_4-S which were increased compared to the situation in the PMull, net losses of Mg, Na, and NO_3-N from the MMor forest were smaller whereas Ca, K, Cl, NH_4-N and PO_4-P accumulated (Table 7.5). Overall, net losses of key nutrients were thus seen to be smaller for the lower-statured MMor forest.

7.5 Discussion

Before assessing the importance of the observed contrasts in nutrient fluxes between the two forests as a determinant of forest stature, the present findings are put into a broader perspective by briefly comparing them with the results obtained for various other tropical montane forest sites.

7.5.1 Nutrient inputs via bulk precipitation and cloud water

Nutrient concentrations in bulk precipitation and cloud water reported for tropical montane forests sites are given in Table 7.6. The pH of the rainfall at Bellevue Peak ranks among the highest observed for montane sites. It approaches the theoretically expected value associated with the dissolution of CO_2 in water (pH = 5.6; *Appelo and Postma* [1993]) and illustrates the pristine character of the rain at this remote site. The low pH values reported for montane forests in Venezuela and Colombia reflect the influence of petrochemical industry [*Steinhardt and Fassbender*, 1979] and volcanic activity [*Veneklaas*, 1990], respectively, and therefore the nutrient concentrations in the rainfall at these sites may be elevated accordingly (notably SO_4-S and possibly Cl). Although a direct comparison of results for different sites is difficult because of differences in rainfall amounts, distance to the ocean, degree of regional forest disturbance (fire), and possibly analytical methods [*Bruijnzeel*, 1989a; *Clark et al.*, 1998], it would seem as though concentrations are lowest at undisturbed high rainfall sites away from the coast (*e.g.* New Guinea, Costa Rica), and highest close to the ocean (Puerto Rico). Nutrient concentrations in the rain at Bellevue Peak generally assume intermediate values, although they tend to be closer to the concentrations observed in inland Costa Rica than those for coastal Puerto Rico (Table 7.6).

As for the cloud water chemistry at Bellevue Peak, there are only few data with which a comparison can be made (Table 7.6). Not unexpectedly, the cloud water in Jamaica had a less 'maritime' character (lower Na, Cl, Mg, SO_4-S) than the fog on an exposed site at 1050 *m* in eastern Puerto Rico [*Asbury et al.*, 1994]. It bore more resemblance to the composition of cloud water at comparable elevations in Venezuela [*Gordon et al.*, 1994] and at 1490 *m* a.s.l. in North-central Costa Rica [*Clark et al.*, 1998] although the present pH is much higher. It cannot be excluded, however, that the concentrations at Bellevue Peak represent a slight underestimate because of the possibility of contamination of the collected cloud water by wind-driven rain (*cf.* Section 4.4.2).

A comparison of the annual atmospheric inputs of nutrients (P+CW) to various montane tropical forests (Table 7.7) shows the Jamaican data to be intermediate again between the very high inputs recorded for a coastal mountain in eastern Puerto Rico [*Asbury et al.*, 1994] and the low inputs to Mount Kerigomna in Papua New Guinea [*Edwards*, 1982]. Inputs via P+CW at Bellevue Peak were generally very similar to those reported for Monteverde, Costa Rica [*Clark et al.*, 1998] although additions of Mg and NO_3-N were distinctly lower in Jamaica. Because the highest and lowest atmospheric nutrient inputs in Table 7.7 were associated with the most stunted (<2–3 *m*; Puerto Rico) and the tallest (30–40 *m*; Papua New Guinea) montane forest, respectively, one must conclude that atmospheric nutrient inputs alone are not reflected by mountain forest stature.

7.5.2 NUTRIENT FLUXES ASSOCIATED WITH NET PRECIPITATION

Nutrient fluxes in net precipitation (*Tf*+*Sf*) in the PMull forest were generally higher than in the MMor forest (Table 7.4). The difference ranged from +9 % for Ca, via +26–31 % for NH_4-N and K to +41 % for SO_4-S. Fluxes of Mg and NO_3-N were slightly smaller (by 8–9 %) in the PMull (Table 7.4). To some extent, the lower values for the MMor forest may be related to the underestimation of corresponding *Tf* volumes signalled earlier (Section 5.6.1) because nutrient concentrations in *Tf* in the two forests were largely comparable (Table 7.2). Even after adding the amounts of nutrients transferred to the forest floor via stemflow (typically 25 % of those in *Tf*), overall nutrient fluxes in the net precipitation in the Jamaican forests proved to be much lower than for most other montane forests (Table 7.7), including those with comparable amounts of net precipitation (Costa Rica, Panama, New Guinea). A glance at Table 7.7 shows that this is largely because nutrient concentrations in the net precipitation in the Jamaican forest are (much) lower than in almost all other montane forests, regardless of their stature. A similar picture emerges from a comparison of (a) the net amounts of nutrients leached from the canopy (*i.e.* nutrients in *Tf*+*Sf* minus those in *P*+*CW*) and, perhaps less clearly, (b) the corresponding enrichment ratios (*i.e.* fluxes in (*Tf*+*Sf*) ÷ (*P*+*CW*)) (Table 7.8).

Of special interest in this respect is that NH_4-N and NO_3-N have been reported to be retained by the canopy in the majority of cases where these elements were included in the analysis, including the present study sites (Tables 7.7 and 7.8). It is likely that the nitrogen is absorbed by the epiphytes and bryophytes that are often so abundant in these montane forests [*Bruijnzeel and Proctor*, 1995]. *Vance and Nadkarni* [1990] demonstrated high microbial biomass and activity (including nitrogen immobilization) in the bryophytic community in the canopy of the Costa Rican forest cited in Tables 7.6–3.12. No such patterns have been observed for P (Table 7.8). It can be concluded, therefore, that amounts of key nutrients cycled through the study forests via net precipitation are among the lowest reported for tropical montane forests. However, such amounts correlate poorly with forest stature, as exemplified by the large contrasts in nutrient amounts carried in net precipitation in forests of comparable stature (*e.g.* Papua New Guinea *vs.* Venezuela) or the similarity in the fluxes for forests of very different stature (*e.g.* Papua New Guinea *vs.* Puerto Rico).

7.5.3 NUTRIENT INPUTS AND LOSSES FROM THE MINERAL SOIL

A closer relationship may be expected, however, between forest stature and amounts of nutrients in litter percolate (*LP*) or topsoil moisture as these should be proportional to the amounts of readily available nutrients. Comparative nutrient concentrations in litter percolates from montane rain forests seem to be limited to those for an intermediate-statured (*c.* 15 *m*) low-altitude forest with Mor humus in East Malaysia [*Bruijnzeel et al.*, 1993] and a tall LMRF in Venezuela [*Steinhardt*, 1979] (see also Table 2.15 in Chapter 2). The cor-

responding estimated annual fluxes are given in Table 7.9A along with those derived for the PMull and MMor forests.

Amounts of K and N_{tot} in litter percolate and possibly NH_4-N and NO_3-N (but not Ca and Mg) parallel the sequence in forest stature for the four forests, *i.e.* Venezuela>Malaysia>PMull>MMor. The role of PO_4-P could not be estimated because of a lack of data for the Venezuelan forest. No clear trend emerges for P_{tot} (Table 7.9A). Equally little information is available on amounts of nutrients lost from tropical montane forests via drainage and much of this information is approximate at best [*Bruijnzeel*, 1991]. The few trends that might be distilled from the litter percolate data (Table 7.9A) no longer exist upon considering nutrient losses via drainage (Table 7.9B). There are some indications that losses of NH_4-N decrease with increasing forest stature and that losses of NO_3-N increase but the dataset is small. Any trends that might exist for Ca, Mg, and K are obscured by geological factors, such as the low base cations in the substrate of the Venezuelan forest (poor sedimentary rock; *Steinhardt* [1979]) and the very high Mg and low K of the ultramafic soils underlying the Malaysian forest [*Bruijnzeel et al.*, 1993] (Table 7.9B).

As pointed out by *Bruijnzeel* [1991], nutrient losses via drainage (streamflow) from tropical forest ecosystems primarily reflect the fertility of the substrate and the amount of drainage/runoff. The estimated losses of Ca, Mg, and K from the two Jamaican forests (Table 7.9B) have been added to the scatter plots of annual runoff/drainage *vs.* nutrient yield for 23 selected (sub)tropical forest ecosystems shown in Fig. 7.6. The position of the Jamaican forests resembles those normally associated with poorer substrates (Ferralsols/Acrisols) rather than their own (Cambisol and Histosol; *cf.* Chapter 2). The significance of this finding is discussed below.

7.5.4 Montane forest stature and nutrient budgets

The general picture emerging from the previous sections is that the two Jamaican forests are cycling less nutrients via precipitation (Tables 7.6–3.12) and, more tentatively though, are losing less nutrients via drainage than intermediate and tall-statured montane forests elsewhere (Table 7.9B). Furthermore, net amounts of nutrients leached from the canopy and the litter layer, and those lost via drainage from the soil of the more stunted forest MMor were generally smaller than in the taller statured PMull forest (Table 7.5). Also, the ranking of concentrations of all major nutrients (notably NH_4-N and NO_3-N) in aqueous extracts from the topsoils in the study area parallelled the ranking according to their stature: WMull>PMull>MMor>Mor (*cf.* Section 7.2 and Table 2.13). A similar result was obtained on the basis of a preliminary comparison of the nutrient concentrations in litter percolate for 3 out of 4 forests: WMull>PMull>MMor (see Section 2.4.4 for details).

However, no such patterns were found when comparing $BaCl_2$-extractable nutrient concentrations or total soil nutrients (Tables 2.10 and 2.11). The reduction in forest stature from WMull to Mor forest was also found to be accompanied by gradually decreasing average concentrations of N, P, K, and Ca

in foliage and leaf litterfall [*Tanner*, 1977a, b] which suggests that each or all of these elements could limit forest growth. A similar trend was observed by *Tanner* [1977a] for exchangeable Ca and K of the mineral soil and for mineral N in the organic topsoils. No trend was found for soil P but significantly increased trunk growth of intermediate-statured 'Mull' forest (rather similar to the present PMull forest) was observed following heavy fertilisation with N (but not for P) [*Tanner et al.*, 1990]. Finally, *Stewart* [1999] reported significantly increased root ingrowth in perlite cores in the Mull forest after addition of N, whereas in the Mor forest this was the case for both N and P.

Thus, the accumulated evidence presented in the foregoing seems to indicate a strong case for forest stature in the area to be controlled by nutrient limitation. However, examination of the nutrient balance sheets for the PMull and MMor forests (Tables 7.10 and 7.11) suggests a somewhat different picture.

As in many other (upper) montane rain forests [*Proctor et al.*, 1989; *Weaver*

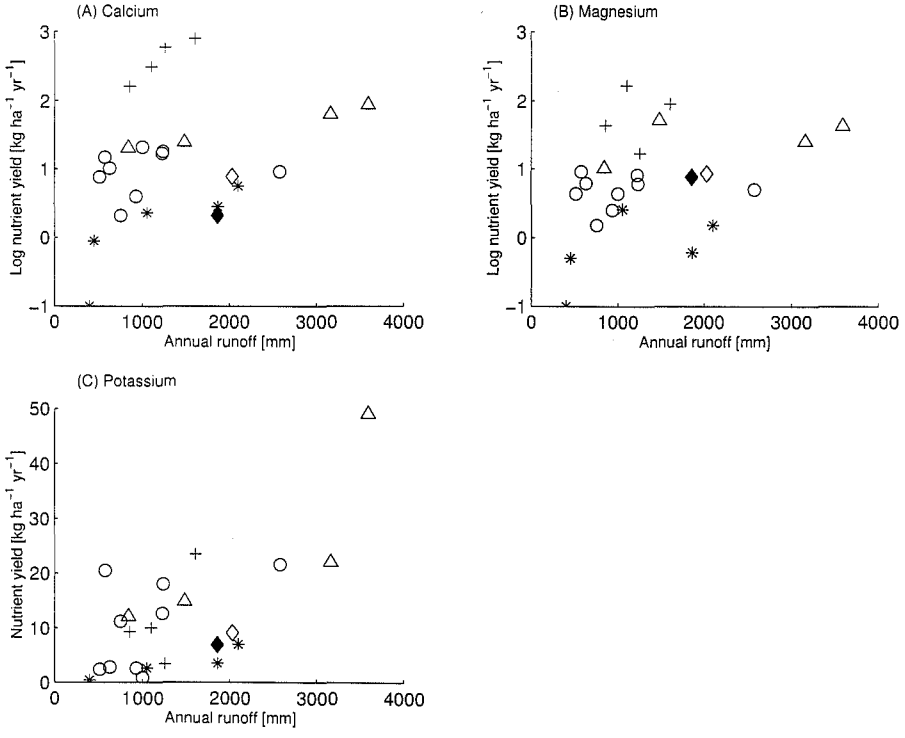

Figure 7.6: Scatter graphs of annual runoff (*mm*) *vs.* (log) annual nutrient yield ($kg\,ha^{-1}\,yr^{-1}$) for selected (sub)tropical forest ecosystems, (A) calcium, (B) magnesium and (C) potassium. Infertile soils (Podzols, Ferralsols) are marked *, + are fertile soils (Rendzinas, Vertisols), ○ Ferralsolsi/Acrisols and △ Cambisols. The PMull (Cambisol) and MMor (Histosol) forests are marked ◊ and ♦, respectively. Non-Jamaican data from *Bruijnzeel* [1991].

et al., 1986], trunk increment rates in the Jamaican forests are low [*Tanner*, 1985]. Although actual stem increment data are lacking for the MMor and the PMull forests, a first approximation may be obtained using measurements of *Tanner* [1985] for the nearby Mor and 'Well-developed' Mull forests, respectively. The associated nutrient immobilization rates ('net uptake'; line 6 in Tables 7.10 and 7.11) are very modest. Indeed, with the exception of P for which atmospheric inputs are very low (line 1 in Tables 7.10 and 7.11), the net uptake of Ca, Mg, K, and N (line 7 in Tables 7.10 and 7.11) represents 22–39 % (PMull) and only 6–12 % (MMor forest) of corresponding amounts in bulk precipitation. Expressed as a fraction of the nutrient fluxes entering the soil in litter percolate (which may be taken as a first approximation of the amounts of *readily available nutrients*) these numbers are reduced even further: $\leq$2 % in the MMor and <4 % in the PMull (line 8 in Tables 7.10 and 7.11). In view of the low inputs of (PO_4)-P in bulk precipitation and cloud water, the relative requirements for net uptake of P are much higher, however, viz. 40 % of atmospheric inputs to the MMor and nearly twice as much in the PMull (line 7 in Table 7.10). From the perspective of net nutrient uptake, it would seem, therefore, that the study forests (with the possible exception of P) will not easily suffer nutrient limitation [*cf.* *Bruijnzeel*, 1989a; *Bruijnzeel et al.*, 1993].

Further support for this contention comes from the fact that inputs of solutes to the soil (carried in *LP* (line 5 in Tables 7.10 and 7.11) greatly exceed solute losses via drainage (line 11 in Tables 7.10 and 7.11), with the exception of mineral N (slight net loss) and Al in the MMor forest (line 12 in Table 7.11). In other words, nutrients seem to accumulate or be retained in the soils of the PMull and the MMor forest, and more so in the PMull (Table 7.10). The forests as a whole were only losing significant net amounts of Mg and Al, presumably as a result of weathering. Net losses of other elements were minor (*e.g.* K in the PMull) or non-existent, *i.e.* net accumulation was again observed (line 13 in Tables 7.10 and 7.11). The net ecosystem gains for P and N concern mineral P and N only because amounts of total P and N in bulk precipitation and cloud water were consistently below the detection limit (*cf.* Table 7.4). The difference in amounts of N_{tot} and mineral N (NH_4-N + NO_3-N) in drainage water was small for the PMull, suggesting that only a small portion of the total nitrogen losses was in an organic form. In the MMor, however, losses of N_{tot} in drainage water were about 150 % of those of mineral N (line 11 in Table 7.11). Here, losses of NH_4-N (1.7 $kg\,ha^{-1}\,yr^{-1}$), NO_3-N (3.0 $kg\,ha^{-1}\,yr^{-1}$) and organic N (2.4 $kg\,ha^{-1}\,yr^{-1}$) were all roughly similar, whereas in the PMull the loss of NH_4-N was about one quarter of the loss of NO_3-N (*cf.* Table 7.4). This finding could be interpreted along the lines of *Northup et al.* [1995] who hypothesized that under conditions of gradually increased soil acidity and reduced nitrogen availability (as is the case in the MMor forest compared to the PMull forest; Table 7.2) forests may bind more mineral N in an organic form to avoid leaching of the more mobile inorganic forms, especially NO_3-N (*cf.* Section 2.4.4).

A net ecosystem accumulation of P based on measurements of PO_4-P in precipitation and drainage/streamflow is commonly observed [*Bruijnzeel*, 1991] and largely reflects the low mobility of the element because of complexation pro-

cesses in the soil [*Sanchez*, 1976]. As indicated earlier (Section 7.5.3), net solute losses from tropical rain forests tend to increase with the fertility of the substrate (Fig. 7.6). Thus far, near-neutral (very slight net losses or gains) nutrient budgets have only been reported for lowland rain forests in Amazonia growing on severely depleted Ferralsols (Oxisols) or Podzols (Spodosols) [*Bruijnzeel*, 1991]. The present soils are not as infertile as those in Amazonia [*cf. Sanchez*, 1976 and Section 2.4.4], yet the forests in Jamaica are not particularly thriving either [*Tanner*, 1985]. However, it would be premature to conclude on the basis of the nutrient budgetary information given in Tables 7.10 and 7.11 that nutrients per se are not limiting growth in the two forests under study, or that, therefore, the trees seem to be unable to make full use of the nutrients that are potentially available [*cf. Bruijnzeel et al.*, 1993]. Nutrient uptake by the trees is not merely associated with trunk growth but also with the production and maintenance of leaves, flowers, seeds, and roots. In the absence of information on below-ground productivity, a first conservative approximation of 'gross' nutrient uptake by the study forests may be obtained by adding the amounts of nutrients in litterfall (line 5 in Tables 7.10 and 7.11) to those incorporated in the stems (line 6 in Tables 7.10 and 7.11). Clearly, the former are much larger than the latter, despite the fact that amounts of K, and to a lesser extent Mg, in litterfall must be seriously underestimated because of leaching from the littertraps [*Proctor*, 1983]. The dynamics of litterfall and the nutrients it contains plus their release by mineralization and decomposition are discussed in some detail in Chapters 8 and 9, respectively. However, it is of interest to note here already that amounts of Ca, Mg, and (presumably) K added annually to the soil in litter percolate are already more than sufficient to cover the corresponding requirements for gross uptake, with the possible exception of Ca in the MMor (line 10 in Table 7.11). Although requirements for both P and N exceed additions in *LP* (roughly by a factor two), the difference between the two forests is slight and cannot be held responsible for their contrast in stature. The present comparison does not include contributions by mineralization and decomposition of litter which will be dealt with in Chapter 9.

Table 7.4: Nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in rainfall (P) and cloud water (CW) at Bellevue Peak, and in throughfall (Tf), stemflow (Sf), litter percolate (LP), soil water in the Ah horizon (SW), and drainage water (D) for the PMull and MMor forests in 1995.

PMull	H	Ca	Mg	K	Na	Al	Fe	Si	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	SO_4-S	Cl
P	0.09	<9.0	<2.0	<8.3	20.6	nd.	nd.	nd.	<3.90	≪1.68	nd.	≪0.13	nd.	≪4.1	34.9
CW	0.00	0.6	0.2	0.2	1.8	nd.	nd.	nd.	<0.10	<0.20	nd.	≪0.01	nd.	0.3	3.1
Tf	0.03	11.2	4.9	34.3	24.4	nd.	nd.	nd.	4.16	≪0.45	nd.	≪0.16	nd.	9.9	42.7
Sf	0.03	2.0	1.0	9.7	5.4	nd.	nd.	0.3	0.55	≪0.22	nd.	≪0.02	nd.	3.1	10.9
LP	0.05	66.7	29.0	108.7	52.1	<4.9	≪2.1	<8.4	5.81	<4.33	27.7	≪0.16	1.40	51.0	111.6
SW_{Ah}	0.45	11.9	14.0	22.0	43.8	16.1	5.2	36.9	4.18	<4.26	18.2	≪0.13	≪0.34	<22.0	57.3
D_{Dw}	0.17	7.7	8.6	9.1	32.0	≪1.8	≪0.9	27.0	<1.50	5.53	8.0	≪0.08	≪0.24	≪6.8	38.9

MMor	H^+	Ca	Mg	K	Na	Al	Fe	Si	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	SO_4-S	Cl
P	0.09	<9.0	<2.0	<8.3	20.6	nd.	nd.	nd.	<3.90	≪1.68	nd.	≪0.13	nd.	≪4.1	34.9
CW	0.00	1.5	0.6	0.6	4.3	nd.	nd.	nd.	<0.25	<0.48	nd.	≪0.03	nd.	0.8	7.6
Tf	0.02	9.0	4.4	23.2	16.5	nd.	nd.	nd.	<3.16	≪0.48	nd.	≪0.15	nd.	<6.9	29.1
Sf	0.01	3.1	2.0	10.1	6.7	nd.	nd.	0.2	0.62	≪0.26	nd.	≪0.03	nd.	<2.4	12.3
LP	0.05	39.3	22.1	68.3	37.0	≪1.9	≪1.1	<3.8	3.03	<1.03	19.3	≪0.19	<0.95	<31.5	65.3
SW_{Ah}	1.72	12.7	18.7	21.5	38.2	35.1	17.6	57.5	3.80	≪2.91	21.5	≪0.09	≪0.62	63.6	69.2
D_{BC}	0.16	≪2.1	7.6	6.9	27.5	6.3	≪0.9	49.7	<1.67	<2.99	7.1	≪0.07	≪0.33	<9.9	33.3

nd.: not determined. The sign '<' is used whenever one of the composite samples showed a concentration below the detection limit, the sign '≪' is used whenever more than three samples had concentrations below the detection limit.

Table 7.5: Net nutrient fluxes (+: net leaching, −: net retention) for different ecosystem compartments in the PMull and MMor forest: (a) forest canopy (fluxes in $Tf+Sf$ minus fluxes in $P+CW$); (b) litter layer (fluxes in LP minus fluxes in $Tf+Sf$); (c) topsoil ($D_{Ah}-LP$); (d) tentire soil profile ($D_{BC}-LP$); and (e) the forest ecosystem ($D_{BC/Bw}$ minus ($P+CW$).

PMull	H	Ca	Mg	K	Na	Al	Fe	Si	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	SO_4-S	Cl
$(Tf+Sf)-(P+CW)$	-0.03	3.6	3.7	35.5	7.4	-	-	0.3	0.8	-1.2	-	0.04	-	8.6	15.6
$LP-(Tf+Sf)$	-0.01	53.5	23.1	64.7	22.3	4.9	2.1	8.1	1.0	3.6	27.7	0.02	1.40	37.9	58.0
$D_{Bw}-(Tf+Sf)$	0.11	-5.5	2.7	-34.9	2.2	1.8	0.9	26.7	-3.3	4.8	8.0	-0.10	0.24	-6.2	-14.7
$D_{Bw}-LP$	0.12	-59.0	-20.4	-99.6	-20.1	-3.1	-1.2	18.6	-4.3	1.2	-19.7	-0.08	-1.16	-44.1	-72.7
$D_{Bw}-(P+CW)$	0.08	-1.9	6.4	0.6	9.6	1.8	0.9	27.0	-2.5	3.6	7.7	-0.06	0.24	-2.4	0.9

MMor	H	Ca	Mg	K	Na	Al	Fe	Si	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	SO_4-S	Cl
$(Tf+Sf)-(P+CW)$	-0.06	1.6	3.8	24.4	-1.7	-	-	0.2	-0.4	-1.4	-	0.02	-	4.4	-1.1
$LP-(Tf+Sf)$	0.02	27.2	15.7	35.0	13.8	1.9	1.1	3.6	-0.8	0.2	19.3	0.01	0.95	22.2	23.9
$D_{BC}-(Tf+Sf)$	0.13	-8.4	5.0	-2.0	2.6	6.3	0.9	49.7	-2.5	5.6	6.8	-0.11	0.23	5.0	-9.2
$D_{BC}-LP$	0.11	-37.2	-14.5	-61.4	-9.5	4.4	-0.2	45.9	-1.3	6.8	-12.2	-0.12	-0.62	-21.6	-32.0
$D_{BC}-(P+CW)$	0.07	-8.4	5.0	-2.0	2.6	6.3	0.9	49.7	-2.5	5.6	6.8	-0.09	0.23	5.0	-9.2

Table 7.6: Volume-weighted mean concentrations of nutrients ($mg\,l^{-1}$) and pH in bulk precipitation (P), cloud water (CW) and throughfall (Tf) in selected tropical montane forests.

Site	Elev.	P/Tf	Vol.	pH	Ca	Mg	K	Na	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	SO_4-S	Cl
	m		mm						[all in $mg\,l^{-1}$]						
Tall LMRF:															
San Eusebio,	2300	P	1576	4.55	0.36	0.33	0.17	0.21	-	-	0.63	-	0.070	0.80	4.5
Venezuela[1]		Tf	1260	5.62	0.55	0.26	5.53	0.35	-	-	0.68	-	0.110	-	-
Altos de Pipa[1a]	1747	CW	-	-	1.10	0.36	0.34	2.84	1.12*	0.27	-	-	-	1.11	3.99
El Avila[1a]	2150	CW	-	-	3.24	0.36	0.38	1.81	2.47*	2.09	-	-	-	1.72	2.71
Kerigomna,	2450	P	$c.$ 3800	-	0.10	0.03	0.19	-	-	-	0.17	-	0.013	-	-
New Guinea[2]		Tf	$c.$ 2585	-	0.87	0.47	3.03	-	-	-	1.40	-	0.117	-	-
Santa Rosa de	2550	P	2115	4.40	0.48	0.15	0.38	1.14	0.86	-	0.85	0.034	-	1.24	0.92
Cabal, Colombia[3]		Tf	1854	5.60	1.45	0.58	5.14	1.45	1.16	-	1.21	0.090	-	2.20	1.96
Cordillera Central,	1200	P	3510	-	0.79	0.12	0.38	1.81	-	-	0.21	0.02	-	0.37	0.98
Panama[4]		Tf	2190	-	1.60	0.35	2.89	5.99	-	-	0.33	0.10	-	0.28	2.26
Monteverde,	1500	P	3191	5.00	0.18	0.07	0.09	0.63	0.05	0.05	-	0.002	-	-	-
Costa Rica[5]		Tf	2068	5.72	1.24	0.43	3.48	2.05	0.07	0.04	-	0.03	-	-	-
		CW	-	4.32	0.67	0.89	0.62	6.42	0.49	0.47	-	0.003	-	-	-
Intermediate UMRF:															
Jamaica[6]	1600	P	2600	-	0.21	0.19	0.27	0.78	-	-	-	-	-	-	-
Mull[6] forest	1600	Tf	2310	-	0.47	0.42	2.33	1.06	-	-	-	-	-	-	-
Jamaica[7]	1849	P	3060	5.52	0.29	0.07	0.27	0.67	0.13	0.06	-	0.004	-	0.14	1.14
		CW	43/104	5.81	1.44	0.57	0.57	4.15	<0.24	<0.46	-	<0.03	-	0.78	7.32
PMull[7] forest	1809	Tf	2233	5.90	0.50	0.22	1.54	1.09	0.19	0.02	-	0.01	-	0.45	1.91
Santa Rosa de	3370	P	1453	4.39	0.51	0.17	0.48	1.10	0.77	-	0.84	0.033	-	1.16	0.94
Cabal, Colombia[3]		Tf	1188	4.39	1.59	0.59	2.78	1.22	0.98	-	0.88	0.034	-	2.67	1.66
Stunted UMRF:															
Jamaica[6]	1600	P	2600	-	0.21	0.19	0.27	0.78	-	-	-	-	-	-	-
Mor[6] forest	1600	Tf	2180	-	0.56	0.53	1.09	1.26	-	-	-	-	-	-	-
Jamaica[7]	1849	P	3060	5.52	0.29	0.07	0.27	0.67	0.13	0.06	-	0.004	-	0.14	1.14
MMor[7] forest	1824	Tf	1821	5.95	0.50	0.24	1.27	0.91	0.17	0.03	-	0.01	-	0.38	1.60
Pico del Este	1050	P	$c.$ 5000	5.19	0.94	0.60	0.53	4.95	0.14	0.11	-	-	-	1.51	6.21
Puerto Rico[8]		Tf	$c.$ 6250†	5.39	1.57	1.32	1.15	10.17	0.08	0.20	1.04	0.004	0.04	2.66	17.68
		CW	$c.$ 460	4.56	1.25	1.06	0.51	9.13	0.44	0.89	0.91	0.001	0.004	2.91	13.63

[1] *Steinhardt* [1979], [1a] *Gordon et al.* [1994], wet season data except *NH_4-N (dry season); [2] *Edwards* [1982]; [3] *Veneklaas* [1990]; [4] *Cavelier et al.* [1997]; [5] *Clark et al.* [1998]; [6] *Tanner* [1977b]; [7] present study; [8] *Asbury et al.* [1994], † a large portion of Tf in Puerto Rico is generated by wind-driven rain [*Weaver*, 1972].

Table 7.7: Annual fluxes of nutrients ($kg\,ha^{-1}\,yr^{-1}$) in rainfall (P), cloud water (CW) and throughfall (Tf) in selected tropical montane forests.

Locality	$P/CW/Tf$	Vol.	H	Ca	Mg	K	Na	NH_4-N	NO_3-N	N_{tot}	PO_4-P	SO_4-S	Cl
		mm						$[kg\,ha^{-1}\,yr^{-1}]$					
Tall LMRF:													
San Eusebio,	P	1576	0.81	5.6	5.2	2.6	3.3	-	-	9.9	1.1†	11.8	59.4
Venezuela	Tf	1260	-	6.9	3.3	69.7	4.4	-	-	8.9	1.4	-	-
Kerigomna,	P	3800	-	3.6	1.3	7.3	-	-	-	6.5	0.5†	-	-
New Guinea	Tf	2585	-	22.6	12.2	78.4	-	-	-	36.1	3.0†	-	-
Santa Rosa, 2550 m	P	2115	0.84	10.1	3.2	7.9	24.1	18.1	-	18.0	0.7	26.2	19.4
Colombia	Tf	1854	0.05	27.1	10.7	95.2	26.9	21.5	-	22.4	1.7	40.9	36.3
Cordillera Central,	P	3510	-	27.9	4.1	13.5	63.5	-	-	7.27	0.70	13.2	34.5
Panama	Tf	2190	-	35.1	7.6	63.2	131.2	-	-	7.18	2.15	6.1	49.6
Monteverde,	P	3191	0.32	5.8	2.4	3.0	20.5	1.7	1.7	-	0.05	-	-
Costa Rica	CW	886	0.17	2.4	3.2	2.2	22.9	1.7	1.7	-	0.02	-	-
	Tf	2068	0.04	23.7	7.8	63.6	41.3	1.3	0.6	-	0.48	-	-
Intermediate UMRF:													
Jamaica[1]	P	2630	-	5.5	5.0	7.1	20.3	-	-	-	-	-	-
Mull[1]	Tf	2310	-	10.8	9.8	55.8	24.4	-	-	-	-	-	-
Jamaica[2]	P	3060	0.09	<8.96	<2.01	<8.34	20.6	<3.9	<1.68	-	<0.13	<4.4	39.4
PMull[2]	CW	43	0.00	0.62	0.25	0.25	1.79	<0.10	<0.20	-	<0.01	0.33	3.15
	$Tf+Sf$	2632	0.06	13.2	5.9	44.0	29.8	4.8	≪0.67	-	≪0.18	13.0	53.6
Santa Rosa, 3370 m	P	1453	0.59	7.3	2.5	6.9	15.9	11.2	-	12.2	0.48	16.9	13.6
Colombia	Tf	1188	0.48	18.8	7.0	33.0	14.4	11.6	-	10.5	0.40	31.7	19.8
Stunted UMRF:													
Jamaica[1]	P	2630	-	5.5	5.0	7.1	20.3	-	-	-	-	-	-
Mor[1]	Tf	2180	-	12.2	11.5	23.7	27.4	-	-	-	-	-	-
Jamaica[2]	P	3060	0.09	<8.96	<2.01	<8.34	20.6	<3.9	<1.68	-	<0.13	<4.4	34.9
MMor[2]	CW	104	0.00	1.49	0.59	0.59	4.32	<0.25	<0.48	-	<0.03	0.81	7.61
	$Tf+Sf$	2380	0.03	12.1	6.4	33.3	23.2	<3.88	≪0.74	-	≪0.18	<9.3	41.4
Pico del Este,	P	5000	0.32	47	30	27	247	6.9	5.3	-	-	38	310
Puerto Rico	CW	460	0.13	5.7	4.9	2.3	42	2.0	4.1	4.2	0.01	13	63
	$Tf+Sf$	6800	0.30	109	91	77	692	5.1	15.2	69	0.24	185	1211

Sites and references as in Table 7.6; [1] *Tanner* [1977b]; [2]present study; [3]concentrations from *Asbury et al.* [1994] times amounts from *Weaver* [1972], a large portion of Tf is generated by wind-driven rain [*Weaver*, 1972]; †total P.

Table 7.8: Estimates of (A) net canopy leaching (*i.e.* nutrient fluxes in *Tf+Sf* minus those in *P+CW*) and (B) relative enrichment of net precipitation (*i.e.* nutrient fluxes in *Tf+Sf* divided by those in *P+CW*) in montane rain forests.

A: Annual net flux ($kg\,ha^{-1}$)

Site	Ca	Mg	K	Na	Cl	NH_4-N	NO_3-N	N_{tot}	PO_4-P	SO_4-S
Tall LMRF										
Venezuela	1.3	-1.9	67.1	1.1	-	-	-	-1.0	0.3[†]	-
New Guinea	19.0	10.9	71.1	-	-	-	-	29.6	2.5[†]	-
Colombia	17.0	7.5	87.3	2.8	16.9	3.2	-	4.4	0.95	14.7
Panama	7.2	3.5	49.7	67.7	15.1	-	-	-0.1	1.45	-7.1
Costa Rica	17.9	5.4	60.6	20.8	-	-0.4	-1.1	-	0.43	-
Intermediate UMRF										
Jamaica										
PMull	3.6	3.6	35.5	7.4	15.6	0.8	-1.2	-	0.04	8.6
Colombia	11.4	4.5	26.1	1.5	6.2	0.4	-	-1.7	-0.1	4.9
Stunted UMRF										
MMor	1.6	3.8	24.4	-1.7	-1.1	-0.4	-1.4	-	0.02	4.4
Puerto Rico	55.3	56.1	47.7	403	838	-3.5	5.8	-	-	134.3

B: Deposition ratios

Site	Ca	Mg	K	Na	Cl	NH_4-N	NO_3-N	N_{tot}	PO_4-P	SO_4-S
Tall LMRF										
Venezuela	1.2	0.64	26.8	1.3	-	-	-	0.9	1.3[†]	-
New Guinea	6.3	9.4	10.7	-	-	-	-	5.6	5.7[†]	-
Colombia	2.7	3.3	12.1	1.1	1.9	1.2	-	1.2	2.3	1.6
Panama	1.3	1.9	4.7	2.1	1.4	-	-	1.0	3.1	0.5
Costa Rica	4.1	3.3	21.2	2.0	-	0.8	0.4	-	9.6	-
Intermediate UMRF										
Jamaica										
PMull[2]	1.4	2.6	5.1	1.3	1.4	1.2	0.4	-	1.3	2.8
Colombia	2.6	2.8	4.8	0.9	1.5	1.0	-	0.9	0.8	1.9
Stunted UMRF										
MMor[2]	1.2	2.5	3.7	0.9	1.0	0.9	0.3	-	1.1	1.8
Puerto Rico[‡]	2.1	2.6	2.6	2.4	3.2	0.6	1.6	-	-	3.6

References as in Table 7.6; [†]net deposition and ratios for total P only. Note that for the contributions via stemflow is minor for the sites in New Guinea, Venezuela, Colombia, Costa Rica and Panama; [‡]The values for Puerto Rico are disturbed as a large portion of *Tf* is generated by wind-driven rain [*Weaver*, 1972].

Table 7.9: Annual fluxes of nutrients ($kg\,ha^{-1}\,yr^{-1}$) in (A) litter percolate and (B) drainage water (or streamflow) in selected tropical montane forests.

A: Fluxes in litter percolate

Locality	Ca	Mg	K	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	Reference
				[all in $kg\,ha^{-1}\,yr^{-1}$]					
Jamaica, MMor	39	22	68	3.0	1.0	19	0.19	1.0	this study
Jamaica, PMull	67	29	109	5.8	4.3	28	0.16	1.4	this study
East Malaysia	118	56	76	17	30	47–110	0.6	1.2	*Bruijnzeel et al.* [1993]
Venezuela	64	26	484	-	-	58	-	3.6	*Steinhardt* [1979]

B: Fluxes in drainage water or streamflow

Locality	Ca	Mg	K	NH_4-N	NO_3-N	N_{tot}	PO_4-P	P_{tot}	Reference
				[all in $kg\,ha^{-1}\,yr^{-1}$]					
Jamaica, MMor	8	8.6	9	1.5	5.5	8	0.08	0.24	this study
Jamaica, PMull	2	7.6	7	1.7	3.0	7	0.07	0.33	this study
East Malaysia*	10	249	2	1	14	-	0.1	-	*Bruijnzeel et al.* [1993]
Venezuela*	1.7	0.6	2.2	-	-	4.4	-	0.3	*Steinhardt* [1979]
Puerto Rico*	43	15	21	-	-	29	-	0.9	*Bruijnzeel* [1991]
Papua New Guinea*	63	25	22	-	-	-	-	-	*Bruijnzeel* [1991]

*Approximate values only; see footnotes in *Bruijnzeel* [1991] and [*Bruijnzeel et al.*, 1993].

Table 7.10: Overview of estimated annual nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in the PMull forest.

(A) PMull forest

	Pathways		Ca	Mg	K	P	N	Al
(1)	Atmospheric input	*P+CW*	9.6	2.2	8.5	0.14*	5.9*	-
(2)	Net precipitation	*Tf+Sf*	13.2	5.9	44.0	0.18*	5.4*	-
(3)	Litterfall	*LF*	50.2	13.2	11.4†	2.9	52.9	5.2
(4)	Total input	*Tf+Sf+LF*	63.4	19.1	55.4	3.1	58.3	5.2
(5)	Readily available nutrients[1]	*LP*	66.7	29.0	108.7	1.4/0.16*	27.7/10.1*	4.9
(6)	Net uptake (immobilization in stems[2])	*NU*	2.6	0.5	2.3	0.11	2.3	-
(7)	*NU* ÷ *P+CW* (%)		27	22	27	79*	39*	-
(8)	*NU* ÷ *LP* (%)		3.9	1.7	2.1	7.9/69*	8.3/23*	-
(9)	Gross uptake	*LF+NU*	52.8	13.7	13.7	3.0	55.2	≥5.2
(10)	Gross uptake ÷ *LP* (%)		79	47	13	214	199	106
(11)	Loss via drainage	*D*	7.7	8.6	9.1	0.24/0.08*	8.0/7.0*	1.8
(12)	Net gain in mineral soil	*LP−D*	59.0	20.4	99.6	1.16/0.08*	19.7/3.1*	3.1
(13)	Net ecosystem gain or loss	*P+CW−D*‡	1.9	-6.4	-0.6	0.06*	-1.1*	-1.8

[1]nutrient flux via litter percolate, *i.e.* arriving at the top of the rooted part of the humus/soil complex; [2]data for 'Well-developed' Mull Ridge forest [*Tanner*, 1985]; * mineral forms only; † seriously underestimated because of leaching from the littertraps; ‡minus sign indicates a net loss.

Table 7.11: Overview of estimated annual nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in the MMor forest.

(B) MMor forest

	Pathways		Ca	Mg	K	P	N	Al
(1)	Atmospheric input	*P+CW*	10.5	2.6	8.9	0.16*	6.3*	-
(2)	Net precipitation	*Tf+Sf*	12.1	6.4	33.3	0.18*	4.5*	-
(3)	Litterfall	*LF*	40.5	11.6	7.9†	2.2	38.6	1.5
	Idem using a decay constant of 0.56°		22.9	6.5	4.4†	1.2	21.6	0.8
(4)	Total input	*Tf+Sf+LF*	52.6	18.0	41.6	2.4	43.1	1.5
	Idem using a decay constant of 0.56°		35.0	12.9	37.7	1.4	26.1	0.8
(5)	Readily available nutrients[1]	*LP*	39.3	22.1	68.3	0.95/0.19*	19.3/4.1*	1.9
(6)	Net uptake (immobilization in stems[2])	*NU*	0.7	0.3	0.5	0.06	0.8	-
(7)	*NU* ÷ *P+CW* (%)		6.7	11	5.6	40*	12*	-
(8)	*NU* ÷ *LP* (%)		1.8	1.4	0.7	6.3/32*	0.4/2*	-
(9)	Gross uptake	*LF+NU*	41.2	11.9	8.4	2.25	39.4	≥1.5
(10)	Gross uptake ÷ *LP* (%)		105	54	12	237	204	79
(11)	Loss via drainage	*D*	2.1	7.6	6.9	0.33/0.07*	7.1/4.7*	6.3
(12)	Net gain in mineral soil	*LP−D*	37.2	14.5	61.4	0.62/0.12*	12.2/-0.6*	-4.4
(13)	Net ecosystem gain or loss	*P+CW−D*‡	8.4	-5.0	2.0	0.09*	1.6*	-6.3

[1]nutrient flux via litter percolate, *i.e.* the nutrients arriving at the top of the rooted part of the humus/soil complex, probably underestimated due to underestimation of *Tf* (*cf.* Section 5.6.1) [2]data for the Mor Ridge forest [*Tanner*, 1985]; °decay constant for total small litter fall (Table 8.3), see Section 8.4.2 for details; *mineral forms only; †seriously underestimated because of leaching from the littertraps; ‡minus sign indicates a net loss.

8

NUTRIENT DYNAMICS IN TWO UPPER MONTANE RAIN FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA. II. DYNAMICS OF SMALL LITTER*

ABSTRACT

To investigate the nutrient dynamics of small litter in two upper montane forests of contrasting stature at c. 1820 m in the Blue Mountains, Jamaica, the quantity and quality of small litterfall, the standing crop of litter on the forest floor, and the annual rates of decay were determined. Despite the considerable physiognomic contrast between the two forests, total inputs of small litter to the forest floor were comparable at 6.5 and 6.2 t ha^{-1} yr^{-1} for the moderately-tall PMull forest (main tree height 7–12 m) and the stunted MMor forest (main tree height 5-8 m), respectively; leaf fall amounted to 79 and 75 % of total litterfall. Mean standing stocks of fine litter were 7.5 and 11.0 t ha^{-1}, respectively. Assuming both forests to be in a steady state, the annual decay rates for total fine litter (k_{tot}) were estimated at 0.87 and 0.59 for the PMull and MMor forests whereas the corresponding decay constants for leaf litter only (k_L) were 1.36 and 0.90, respectively. Annual nutrient accession rates via total small litterfall in the PMull and MMor were: 53 and 39 kg ha^{-1} yr^{-1}, respectively; 3 and 2 kg ha^{-1} yr^{-1} for P; 50 and 40 for Ca, 11 and 8 for K; 13 and 12 for Mg; and 5 and 2 kg ha^{-1} yr^{-1} for Al. Concentrations of N, P and major cations were all significantly higher in PMull leaf litterfall; aluminium concentrations in the latter were 3–4 times those in the MMor. Concentrations of phenols in leaf fall were c. 30 % higher (not significant) in the MMor site. The inter-site contrasts were reduced or absent in the trash- and woody litterfall fractions as well as in live foliage. Nutrient fluxes in litterfall of N and K were low, and fluxes of P, Ca, and Mg relatively high compared to montane forests elsewhere, but high when compared to element accession rates observed in very stunted cloud forest ('elfin' forest).

The increased phenolic concentrations in leaf fall in the MMor forest are probably related to pH–Al induced stresses and have multiple effects on forest functioning.

*With: L. A. Bruijnzeel. A slightly modified version of this chapter (Part II in a series of three) will be submitted to the *Journal of Ecology*

8.1 INTRODUCTION

Many (but not all) tropical upper montane forest soils are characterized by persistently wet conditions, shallow root systems, high acidity, and low levels of available nutrients, notably N [*Bruijnzeel and Proctor*, 1995]. Litterfall and litter decomposition thus constitute a major pathway via which organic matter and nutrients (perhaps with the exception of K which is also cycled effectively via net precipitation) are supplied to the soil [*Vitousek and Sanford*, 1986; *Proctor*, 1987]. High acidity, and low soil fertility may adversely affect the quality of litter, both in terms of nutrient concentrations and amounts of secondary organic compounds such as phenols, with negative implications for the decomposing communities and mineralization of organic matter [*Coulson et al.*, 1960; *Kuiters*, 1990]. Ectorganic material may thus become recalcitrant to decomposition and accumulate on top of the mineral soil which, in turn, further restricts the release and availability of basic elements [*Coulson et al.*, 1960; *Verhoef and Brussaard*, 1990]. On the other hand, *Northup et al.* [1995] suggested that complexation of mobile N ions by polyphenols could reduce their depletion via leaching. Polyphenols may also form complexes with 'free' aluminium in acid soils which reduces aluminium toxicity and may decrease the fixation of phosphorus by Al [*Hue et al.*, 1986].

Topsoil (Ah-horizons) acidity in Jamaica's montane forests ranges from pH 4.2 in the Mull-type soils to pH 3.4 in the Mor-type soils ([*cf. Tanner*, 1977a, Fig. 2.7]. Concentrations of phenols and total Al in topsoil moisture in Mor-type forest were demonstrated to be three times those found in Mull-type forests (Table 2.12) whereas amounts of toxic Al^{3+} were estimated to be up to ten times higher (see Fig. 2.9). Finally, amounts of inorganic N in litter percolate and topsoil water were higher in Mull -type forests than in Mor-type forests whereas dissolved organic N (DON) exhibited a reverse pattern (Table 2.12) conform the hypothesis of *Northup et al.* [1995].

The nutrient fluxes associated with hydrological pathways in two upper montane rain forests of contrasting stature at *c.* 1820 *m* a.s.l. in the Blue Mountains of Jamaica (relatively tall PMull forest and short-statured MMor forest) have been described in the previous chapter (Chapter 7, part I in this series of three). It was demonstrated, *inter alia*, that the *net* uptake of nutrients (approximated by the amounts of nutrients immobilized annually in stem increment) by the two forests constituted only a small fraction of the corresponding fluxes of solutes (*i.e.* readily available elements) leached from the more or less undecomposed litter at the top of the soil profile. The latter amounts also equalled or exceeded the annual *gross* uptake (defined as net uptake plus small litterfall) of Ca, Mg, and K, but not of P and N, in both forests. The aim of the present chapter (part II in the series) is to provide information on the amounts and quality of the small litter produced by the PMull and MMor forests (including contents of Al and phenols), and to derive an initial estimate of litter decay rates and thus of

additional nutrient release. More detailed information on litter decomposition and soil biotic activity will be given in Chapter 9 (part III in the series).

8.2 STUDY SITES

The physiognomy, floristics and soils of the two study forests have been described in detail in Chapter 2 whereas a summary has been given in part 1 of this series (Chapter 7). Suffice to state here that in the PMull forest a discontinuous ectorganic horizon (litter and fragmentation layers <4 *cm*) plus a thin layer of mull humus (*c.* 2 *cm*) overlie a leached clayey mineral soil (Dystric cambisol). The soil in the MMor forest is characterized by a thick high-surface root mat and accumulation of slowly decomposing mor-like humus (thickness ≤ 50 *cm*) on top of a shallow soil profile (Folic histosol; $\simeq$ 70 *cm*). The pH_{H_2O} of litter in the PMull is 5.1–5.6, compared to 4.7 for MMor litter. Values within the aluminium buffer range (pH 2.4–3.8) are observed in the lower part of the MMor ectorganic layers.

The PMull and MMor forests show a considerable overlap in tree species. Principal species include *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, *Clethra occidentalis*, *Chaetocarpus globosus*, *Alchornea latifolia* and *Podocarpus urbanii*. Mor-type forest is characterized by relatively large numbers of *L. octandra* and the terrestrial epiphyte *Clusia* cf. *havetioides*. On the other hand, the species *C. occidentalis*, *P. urbanii* and *Hedyosmum arborescens* are more typical for the Mull sites [*Tanner*, 1977a] (see also Section 2.3.1). The dominant leaf size is microphyllous/notophyllous. The leaves are hard and leathery and considered xeromorphic [*Tanner and Kapos*, 1982]. The leaf area index (LAI) of the PMull forest was estimated at 5.0 (Section 4.4.3) *vs.* 4.1 for the MMor forest (Table 2.1)

8.3 METHODS

Litterfall

The PMull and MMor forests were equipped with nine randomly located litter traps consisting of a well-draining 0.8×0.8 *m* nylon netting (mesh width 1 *mm*) supported by a bamboo frame placed *c.* 40 *cm* above the forest floor and sloping *c.* 30 *cm* towards the centre in order to keep the litter trapped. Accumulated litter was collected between 8 April 1995 and 9 April 1996 and retrieved every 3 to 4 weeks. Branches were included as wood fall; no wood fall with diameter ≥ 5 *cm* along the shortest axis was observed. All material was air-dried at the Cinchona field station until transportation to the laboratory in Kingston where the collections were oven-dried at 50 °C to constant weight. This low drying temperature was maintained to prevent evaporation of phenolic compounds [*Kuiters*, 1990]. Collections were sieved over a 4×4 *mm* wire mesh to separate 'trash' (including all reproductive parts) from leaves, wood and epiphytic material. Wood fall included all twigs (of any size), branches and bark. All fractions were weighed separately to the nearest 0.001 *g*. Leaf litter was bulked per plot (9 traps) and thoroughly mixed. A sub-sample (30–50 % of

the total) was sorted to evaluate the contributions by the principal tree species (eleven species for MMor material *vs.* 13 for PMull leaves). Sub-samples were remixed, coarsely ground and stored until analysis in Amsterdam where samples were redried (50 $^{\circ}C$, 24 h) and ground in a centrifugal ball mill. One collection (no. 2, collected on 11 June 1995) was lost for chemical analysis due to a malfunctioning oven. Samples were digested in $HNO_3/HClO_4$ at 150 $^{\circ}C$ for 25 *min.* using the microwave/pressure bomb method [*Smit*, 1995]. Digestions were analyzed for P, Ca, K, Mg, and Al by ICP-AES emission (Perkin-Elmer 6500). The quality of digestion and analyses were checked against one sample of reference material (olive leaves, *Olea europaea*; BCR-CRM 062. no. 0535) and one blank sample per 10 samples. Nitrogen and carbon were determined using a Carlo Erba 1600 elemental analyzer. Phenolic compounds were determined using the method described by *Box* [1983] and *Waterman and Mole* [1994]. Samples of 0.10 g were extracted for 1 h in aqueous methanol (8.0 ml, 50 % by volume). Phenol concentrations were determined photometrically using Folin-Ciocalteau reagents (Merck, art. nr 1.09001.0100). Absorbance was measured at 760 nm relative to a solution series of pure tannic acid powder (Merck, art. nr 1.00773.0250). Concentrations of phenolic compounds were expressed as tannic acid equivalents (TAE).

Litter standing crop

Although litter standing crop (LSC) is subject to temporal variability, it was decided to determine LSC only on one occasion (April 1996) because of the relatively large disturbance of the sampling to the forest floor. Within 30 randomly located quadrants (0.40 × 0.40 m) all litter (including all wood $\leq$5 cm along the shortest axis) down to the fragmented litter (F-) layer was removed from the forest floor, placed in bags, and oven-dried (80 $^{\circ}C$) to constant weight. Collections were sorted for wood and non-wood (mainly leaves and reproductive parts) and weighed to the nearest 0.1 g.

Litter accumulates on the forest floor until litterfall equals the rate of decomposition, after which the standing crop of litter on the forest floor will oscillate around a steady-state mean value [*Ewel*, 1976]. Assuming such a steady-state condition, a first estimate of the litter decomposition rate can be obtained by dividing the amount of annual litterfall (LF, $t\,ha^{-1}\,yr^{-1}$) by the litter standing crop (LSC, $t\,ha^{-1}$). The litterfall decomposition (or decay) constant k_L, which is an approximation of the fraction of the litter standing crop that decomposes in one year, therefore equals [*Anderson and Swift*, 1983]:

$$k_L = \frac{LF}{LSC} \tag{8.1}$$

Live foliage

Live foliage of eight principal tree species (Euphorbiaceae: *Alchornea latifolia*, *Chaetocarpus globosus*; Clethraceae: *Clethra occidentalis*; Guttiferae: *Clusia* cf. *havetioides*; Cyrillaceae: *Cyrilla racemiflora*; Podocarpaceae: *Podocarpus urbanii*; Ericaceae: *Lyonia* cf. *octandra*, *Vaccinium meridionale*) was sampled in December 1994. Twenty to forty mature, sunlit leaves without signs of

herbivory or discolouring were taken from each of 4–6 trees per species per site. Leaves were bagged separately by tree, dried at 50 $^{\circ}C$ to constant weight and ground. Sub-samples were processed and analyzed for nutrients and phenolic compounds as described for the litter samples. Mean nutrient concentrations of live foliage for each forest were calculated by weighing the individual means for species (mean of $n = 5$ trees) by their contribution to annual leaf litterfall.

Statistical analyses
Analyses of variance (ANOVA) were used to determine inter-site differences; *t-test* statistics [*Sokal and Rohlf*, 1981] were applied when sample sizes were small [*Spiegel*, 1972]. Both refer to 95 % probability levels. Distribution-free or non-parametric statistics [*Natrella*, 1963] were used to determine contrasts between various fractions of litterfall. Correlations (at 95 % probability levels) refer to linear regressions (non-transformed data) unless stated otherwise.

8.4 Results

8.4.1 Litterfall

Despite being very different in terms of physiognomy and edaphic conditions (*cf.* Chapter 2), the Mor and PMull forests had very similar total and leaf litterfall (Table 8.1). The seasonal patterns of both leaf- and total litterfall for the two forests also resembled each other, with maximum values in May–July and a minimum in September (Fig. 8.1). Total annual litter production was 6.47 $t\,ha^{-1}$ in the PMull forest and 6.16 $t\,ha^{-1}$ in the MMor whereas leaf fall in the PMull was about 10 % higher (5.12 *vs.* 4.62 $t\,ha^{-1}\,yr^{-1}$). Although one-way ANOVA showed no significant differences between the two forests for any of the fractions. A *t-test* analysis of spatial data ($n = 9$ traps) suggested that annual trash litterfall was significantly higher in the PMull ($P< 0.01$). Wood and epiphyte fall were marginally larger in the MMor site but not significantly so due to the large temporal and spatial variation. Trash fall was significantly higher in the PMull. Wood fall larger than ≤ 5 *cm* along the shortest axis and tree fall were not observed during the 1995–1996 observation period.

Leaf fall contributed 79 and 75 % of total litter in the PMull and MMor, respectively. In both forests the amounts of total litterfall and leaf fall were significantly correlated ($P<0.001$, $r^2 = 0.64$ and 0.83 for PMull and MMor, respectively). Corresponding values for wood fall ≤ 5 *cm* were 9 and 15 %; for trash fall (mainly reproductive parts) 11 and 7 % ; and for epiphytes 0.85 and 2.2 % (55 and 138 $kg\,ha^{-1}\,yr^{-1}$). Both amounts of total litterfall and total leaf fall ($n = 13$ mean values of 9 traps per forest) were closely correlated between the two forests ($r^2> 0.80$, $P< 0.0001$), To a lesser extent this was also the case for trash litterfall ($P< 0.01$, $r^2 = 0.62$) and wood litterfall ($P< 0.05$, $r^2 = 0.32$). Amounts of epiphyte fall showed no significant correlation between forests, illustrating the rather more random character of the process (*cf.* the high CoV's associated with epiphyte fall in Table 8.1). Because epiphytic growth is usually concentrated on branches, some relationship between wood-

Table 8.1: Mean annual production ($t\,ha^{-1}\,yr^{-1}$) of leaf, wood and trash fractions in total litterfall in the PMull and MMor forests as collected between 8 April 1995 and 9 April 1996. Woody fraction includes all wood collected ($\leq$ 5 *cm* diameter). The coefficients of variation (CoV; percentage of the mean) were obtained using both spatial ($n = 9$), and temporal ($n = 13$) data, the latter being weighed for duration.

Forest	Leaf	CoV		Wood	CoV		Trash	CoV	
	$t\,ha^{-1}$	spat.	temp.	$t\,ha^{-1}$	spat.	temp.	$t\,ha^{-1}$	spat.	temp.
PMull	5.12	11	55	0.58	51	86	0.72	29	45
MMor	4.62	27	58	0.94	67	105	0.46	34	40

Forest	Epiphytes	CoV		Total	CoV	
	$t\,ha^{-1}$	spat.	temp.	$t\,ha^{-1}$	spat.	temp.
PMull	0.06	111	131	6.47	14	42
MMor	0.14	160	187	6.16	25	46

and epiphyte fall was expected but a significant positive correlation ($r^2 = 0.36$, P<0.05, $n = 13$) was observed for the PMull forest only.

Wood and epiphyte litterfall (mainly bromeliads) both showed a high degree of spatial variability (Table 8.1). Median values ($n = 9$ traps per forest) fell far below the corresponding arithmetic means. Using median values, the calculated annual wood fall in the PMull and MMor forests would be 44 % and 62 % less than based on the spatial averages listed in Table 8.1. For epiphytes the reductions would amount to 81 % and 93 %, *vs.* 12 % and 9 % for thrash, and 1.6 % and 6 % for leaves in the PMull and MMor forest, respectively; total litter production would be lowered by *c.* 2.4 % (PMull) and 11.0 % (MMor). More reliable estimates of wood- and epiphytefall would therefore require a more intensive sampling program using more traps [*cf.* *Tanner*, 1980a].

Although litterfall for all fractions showed temporal fluctuations, no marked seasonal patterns were found for wood, trash and epiphytes (Fig. 8.1). Leaf shedding, however, appeared to be inversely related to the annual distribution of rainfall (Fig. 8.2; $r^2 = 0.39$ and 0.47 (P< 0.05), for PMull and MMor forest, respectively). Mean daily leaf fall rates during the relatively dry period April–June 1995 ($\overline{P}$ =3.7 $mm\,d^{-1}$) were three to four times higher (at *c.* 2.6 $g\,m^{-2}\,d^{-1}$ *vs.* *c.* 0.7 $g\,m^{-2}\,d^{-1}$) than during the wet months September–December ($\overline{P} = 11.8\ mm\,d^{-1}$). A similar relationship between rainfall and total litterfall was not significant, however.

Temporal patterns of plant species contribution to leaf fall could be determined for more than 90 % of the collected leaf litter. The seven principal species listed in Table 8.2 made up 78.3 % (PMull) and 80.4 % (MMor) of total leaf fall. *Cyrilla racemiflora* dominated leaf fall for most of the year in both forests (Table 8.2), followed by *Lyonia* cf. *octandra* in the MMor and *Alchornea latifolia* in the PMull. Besides the species listed in Table 8.2, noticeable leaf fall was generated in the PMull by *Dendropanax arboreus* and *Podocarpus urbanii* (3.5 % and 1.7 % of total leaf fall), and in the MMor forest by the introduced species *Cinchona pubescens* and *Pittosporum undulatum* (5.4 % and 4.4 %).

The species specific contribution to leaf fall showed only moderate seasonal-

Table 8.2: The mean percentage contribution to annual leaf litterfall by seven principal tree species and their maximum contribution (for one 3–4 week period). The species included are: *Alchornea latifolia*, *Chaetocarpus globosus*, *Clethra occidentalis*, *Clusia* cf. *havetioides*, *Cyrilla racemiflora*, *Lyonia* cf. *octandra*, and *Vaccinium meridionale*.

Forest		Alc.	Cha.	Cle.	Clu.	Cyr.	Lyo.	Vac.	others
		[% of total annual leaf litterfall]							
PMull	mean	18.0	10.4	9.0	7.1	25.8	6.3	1.7	21.7
	max.	30.5	17.5	37.1	13.5	36.0	13.0	8.9	38.4
MMor	mean	1.1	5.5	7.5	8.4	28.0	23.3	6.6	19.6
	max.	2.9	8.5	35.4	19.1	44.4	41.5	16.1	44.9

ity. The maximum contribution to total leaf fall was typically twice the average annual contribution (Table 8.2). *Clethra occidentalis* was the only species with a distinct seasonal pattern of leaf shedding. Its leaf fall was concentrated around January–February. Annual leaf contributions to leaf fall were significantly correlated with basal area contributions ($r^2 = 0.70$, $P < 0.01$ for the PMull; $r^2 = 0.59$, $P < 0.05$ for the MMor) and stem density (PMull: $r^2 = 0.44$, $P < 0.05$; MMor: $r^2 = 0.52$, $P < 0.05$) (*cf.* Table 2.2).

8.4.2 Litter standing crop

The standing crop of small litter (leaves, trash and epiphytic remains) as determined in April 1996 was significantly higher (33 %) in the MMor forest (one-tail *t-test*, $\alpha = 0.05$, $P < 0.001$; $n = 30$ per site; Table 8.3). Amounts of woody or total litter were not significantly different between the plots. Standing crops of leaves/trash and woody litter were not significantly correlated. The total litter standing crop was equivalent to 115 % (PMull) and 178 % (MMor) of the corresponding annual small litterfall. For leaves+trash these ratios reduced to 75 % and 113 % of the respective annual inputs.

Assuming that both forests are in a steady state, the decomposition constant or decay rate k_L can be approximated by the amount of annual litter input divided by the litter standing crop (Eq. 8.1). At $k_L = 1.36$, 9 months are suggested to be sufficient to decompose the estimated annual addition of leaf litterfall in the PMull, which may explain the irregular (occasionally absent) character of the litter layer in Mull-type forests in the area [*Grubb and Tanner*, 1976; *Spijkerman*, 1996]. At $k_L = 0.9$, the decay rate derived for the MMor forest suggests a considerably slower decay rate which agrees with the observed edaphic traits for the Mor-type forests, *i.e.* a (more or less) substantial accumulation of organic matter [*Grubb and Tanner*, 1976; *Spijkerman*, 1996]. For woody litter, the decay constants indicate a residence time of approximately 5 years for both the PMull and the MMor. As a result, k_L for total litter becomes <1.0 in both forests but the considerable inter-site contrast derived earlier for small litter remains (Table 8.3).

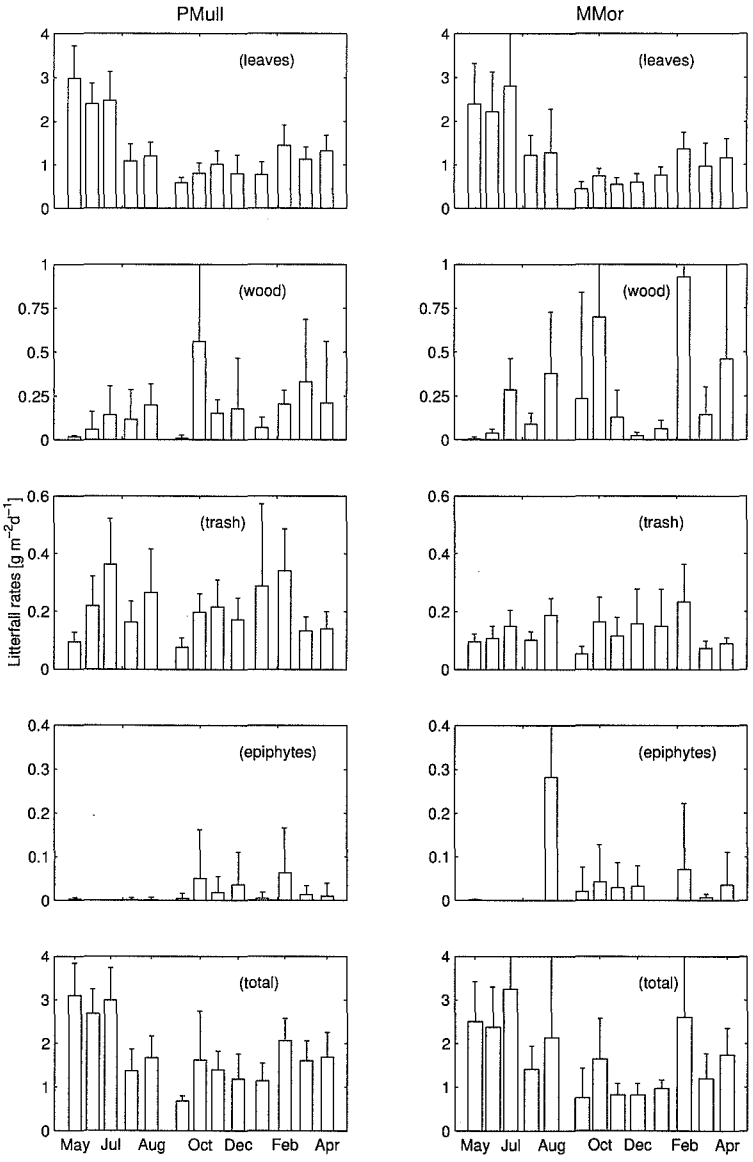

Figure 8.1: Seasonal variation in mean litterfall rates ($g\,m^{-2}\,d^{-1}$) for leaf, small wood, trash, and epiphytic litter fractions collected at 3–4 week intervals between 8 April 1995 and 9 April 1996 in the PMull and MMor forests. Vertical lines represent one standard deviation about the mean ($n = 9$ traps per site).

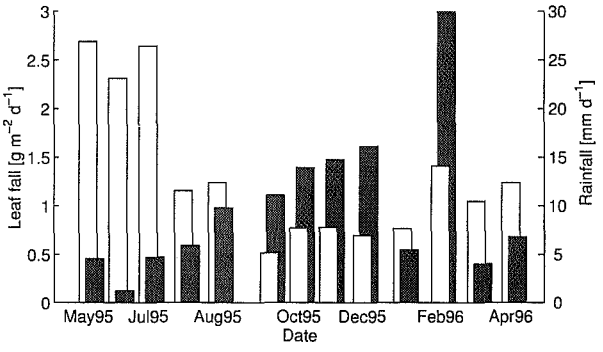

Figure 8.2: Average monthly leaf fall rates ($g\,m^{-2}\,d^{-1}$; light bars) in the PMull and MMor forests in relation to average daily precipitation ($mm\,d^{-1}$; dark bars) for corresponding periods.

Table 8.3: Mean dry mass of litter standing crop (LSC, $t\,ha^{-1}$) with standard deviations in parentheses ($n = 30$ samples of 0.16 m^2 each per plot) in the PMull and MMor forests in April 1996, plus the corresponding annual litter inputs ($t\,ha^{-1}\,yr^{-1}$) and derived decomposition constants k_L. The small litter fraction includes leaves, trash and epiphytic litter; the wood fraction consists branches with diameter ≤ 5 *cm*.

Forest	Litter fraction	LSC [$t\,ha^{-1}\,yr^{-1}$] mean	s.d.	Range [$t\,ha^{-1}\,yr^{-1}$]	Annual input [$t\,ha^{-1}\,yr^{-1}$]	k_L [-]
PMull	small	4.3	(1.4)	1.6–7.5	5.9	1.36
	wood	3.1^{ns}	(3.6)	0.4–16.1	0.6	0.19
	total	7.5^{ns}	(3.9)	2.0–20.9	6.5	0.87
MMor	small	5.8^{**}	(1.7)	3.6–9.7	5.2	0.90
	wood	5.3^{ns}	(7.7)	0.3–42.8	0.9	0.18
	total	11.0^{ns}	(8.2)	5.2–50.7	6.2	0.56

**: significant at P< 0.001; ^{ns}: not significant.

Naturally, these estimates are based on a single collection only and as such they should be treated with caution. However, as shown in Fig. 8.1, leaf fall in February–April 1996 was approximately average. Furthermore, the fact that the relative magnitudes of the derived values of k_L agree with field observations of forest floor characteristics lends some support to their credibility.

8.4.3 Nutrient concentrations in litterfall

Elemental concentrations in leaf litterfall were consistently lower in the short-statured MMor forest (Table 8.4), with the largest contrasts being found for N, P, Ca and K (all *c.* 20 % less compared to leaf fall in the PMull). These contrasts tended to be reduced (N and K) or reversed (P, Ca, and Mg) in the trash fractions but concentrations in wood fall, again, tended to be higher in the

PMull (typically by >30 %). By contrast, mean concentrations of phenols were 28 % higher in MMor-type leaf litter but the differences were not significant (*t-test* analyses, $\alpha = 0.95\%$, P>0.05, $n = 12$). For aluminium concentrations in leaf fall the contrasts were striking: Al in PMull leaf litter (0.59–1.39 $mg\,g^{-1}$) was approximately four times that in MMor leaf litter (0.15–0.36 $mg\,g^{-1}$). The difference was significant at P< 0.001. Contrasts for trash and woody material were less distinct (and not significant). In both the PMull and MMor forest, K, N and P were significantly higher in the trash fall fraction ($\alpha = 0.01$, rank sum maximum test, *Natrella* [1963]) whereas Mg and Al were higher in the leaf litter fraction of the PMull forest only ($\alpha = 0.05$). Nutrient concentrations in the leaf and trash fractions were not correlated with corresponding rates of litter production, except for a negative correlation between nitrogen concentrations and leaf fall (PMull: $r^2 = 0.38$, P<0.05; MMor: $r^2 = 0.48$, P<0.05).

Nutrient concentrations in leaf and trash fall showed considerable seasonal fluctuations but the patterns were not consistent for all elements (Figs. 8.3 and 8.4). Any 'trends' have to be interpreted with care as nutrient concentrations in litter reflect (i) initial foliar concentrations, (ii) retranslocation strategies prior to abscission, as well as (iii) leaching losses (especially for K) from the trapped litter [*Proctor*, 1983].

Despite these restrictions, some interesting patterns emerged: the temporary increase of C in trash- and leaf litter during November–February was paralleled by Ca and Mg in leaf litter but the opposite was observed in trash fall. The correlations between Ca, Mg, and C were positive and significant for PMull- but not for MMor leaf fall. Nitrogen and P in leaf fall which were highly correlated in both forests (PMull: $r^2 = 0.81$, P< 0.0001; MMor: $r^2 = 0.48$, P< 0.05) increased steadily during the summer months, only to reduce again after December. Again, an opposite trend was found for the trash fraction. Furthermore, phosphorus concentrations in leaf fall appeared to be significantly correlated with concentrations of K and phenols (r^2> 0.41, P< 0.05). Nitrogen concentrations were mirrored by those of K in the PMull ($r^2 = 0.40$, P< 0.05) but not in the MMor ($r^2 < 0.2$). Concentrations of Ca and Mg were correlated only for leaf fall in the PMull forest ($r^2 = 0.52$, P< 0.01). Interestingly, Al in leaf fall from the MMor was significantly correlated with P, N, (positive) and polyphenols (negative) (r^2> 0.34, P< 0.05) whereas no such relationships were found in leaf fall in the PMull. Concentrations of phenolic compounds in leaves mirrored those for nitrogen (PMull: $r^2 = 0.55$, P< 0.01; MMor: $r^2 = 0.34$, P< 0.05).

Short temporary drops in concentrations were found in PMull and MMor trash litterfall for P (reduction by 30 %), K (down by 50 % in MMor only) and in particular Ca and Mg (reductions of 50 and 30 %) at the end of the 1995 wet season (August–December) when litter production was at a minimum (*cf.* Fig. 8.2 and Fig. 8.4). This trend was reflected by a temporary increase in carbon content (to 52 % *vs.* 47 % during the rest of the year). Concentrations of C in trash litterfall were significantly (and negatively) correlated with those of K, Ca, Mg and P (and N in the MMor) ($r^2 = 0.38 - 0.77$, P< 0.05) but the correlations for MMor material were typically better that for PMull trash. Similar patterns

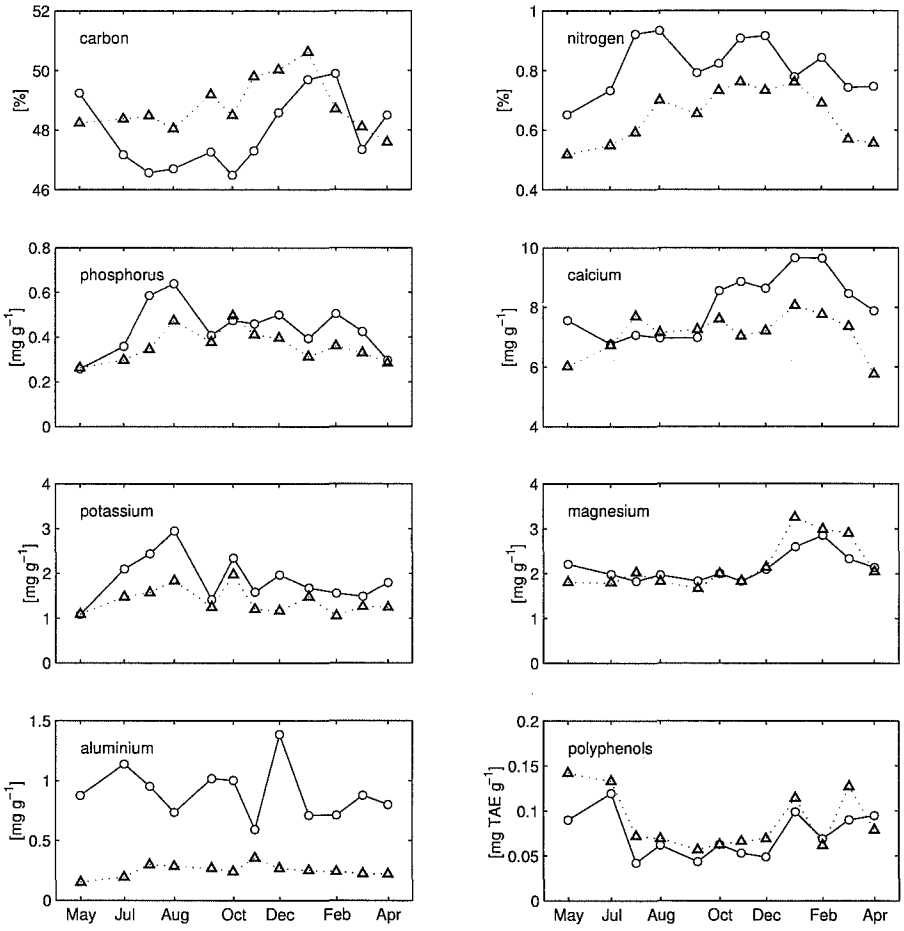

Figure 8.3: Seasonal fluctuations of nutrient concentrations ($mg\,g^{-1}$) in leaf litter collected at 3–4 week intervals between 8 April 1995 and 9 April 1996 in the PMull (circles) and MMor (triangles) forests. Concentrations of C and N expressed as percentage dry weight; phenolic compounds as $mg\,\mathrm{TAE}\,g^{-1}$.

were found for phosphorus (highly significant, positive, correlations with Ca, K, Mg, and N ($r^2 = 0.69 - 0.84$, P< 0.001) in the MMor and more moderate correlations with K, Mg and N in the PMull ($r^2 = 0.41 - 0.65$, P< 0.05)) and for N (significant correlations with Mg, Ca, and K in the MMor ($r^2 > 0.56$, P< 0.01) *vs.* a weak correlation with Mg in the PMull ($r^2 = 0.44$, P< 0.05)). The relationship between concentrations of Ca and Mg was only significant (but very robust) in trash litterfall from the MMor ($r^2 = 0.84$, P< 0.0001) whereas (weak) correlations between phenols and K, Mg, and N were observed in trash litterfall from the PMull only ($r^2 = 0.36 - 0.45$, P< 0.05). Finally, nutrient

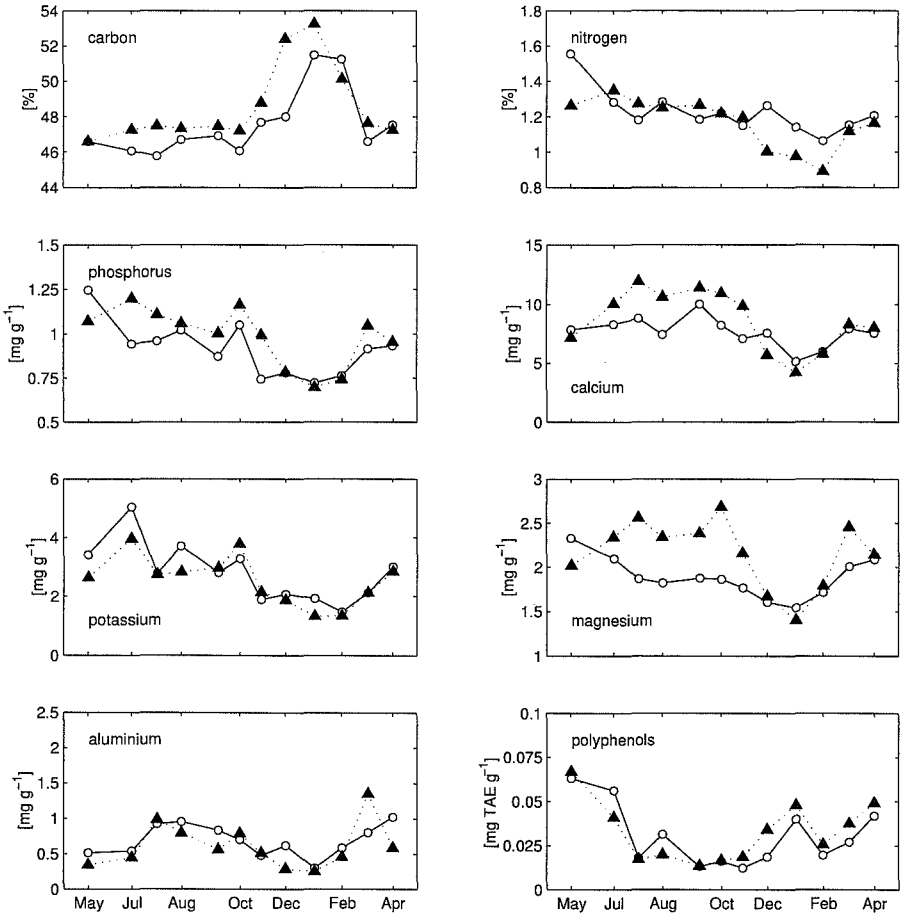

Figure 8.4: Seasonal fluctuations of nutrient concentrations ($mg\,g^{-1}$) in trash litterfall collected at 3–4 week intervals between 8 April 1995 and 9 April 1996 in the PMull (circles) and MMor (triangles) forests. Concentrations of C and N expressed as percentage dry weight; phenolic compounds as $mg\,\mathrm{TAE}\,g^{-1}$.

concentrations in both leaf- and thrash litterfall (including those for K, P, and N) were not correlated with rainfall amounts.

8.4.4 Nutrient fluxes in litterfall

Estimated annual fluxes of N, P, Ca, K, and Mg in leaf-, trash-, and total litterfall (Table 8.5) were all higher in the PMull forest whereas fluxes via wood fall were higher in the MMor (for N, P, Ca, and Al), despite the consistently lower element concentrations in woody litterfall in the MMor (Table 8.4). Contrasts in total element fluxes were small for carbon (*c.* 5 % higher in the PMull); the

Table 8.4: Weighed mean concentrations (in $mg\,g^{-1}$) and their temporal standard deviations (SD; $n = 12$ collections) of nutrients in leaf-, trash- and wood fall fractions. Differences per category between forest types were tested for significance by *t-test* analysis ($n = 12$ paired samples). Data on woody litterfall represent a two-sample average only. Concentrations of carbon in gg^{-1}; polyphenols in $mg\,\mathrm{TAE}\,g^{-1}$.

Forest	Fraction	C	N	P	Ca	K	Mg	Al	Phenols
PMull	leaf	0.48	7.73^{c}	0.40^{a}	7.89^{b}	1.72^{b}	2.16	0.90^{c}	80
	SD.	0.01	1.00	0.12	0.95	0.54	0.29	0.18	23
	trash	0.48	12.09	0.89	7.31	2.78	1.85^{a}	0.65	31
	SD.	0.02	1.13	0.14	1.27	1.11	0.21	0.22	16
	wood	0.47	8.02	0.37	7.96	1.06	1.47	0.27	9.0
MMor	leaf	0.49	6.09^{c}	0.33^{a}	6.89^{b}	1.34^{b}	2.12	0.22^{c}	102
	SD.	0.01	1.85	0.07	0.73	0.26	0.50	0.05	34
	trash	0.49	11.35	0.96	8.20	2.42	2.09^{a}	0.57	33
	SD.	0.02	1.53	0.17	2.53	0.87	0.39	0.28	16
	wood	0.47	5.52	0.28	5.19	0.58	0.91	0.22	10

Significant differences per category between forests are indicated by the same letter: $^{a}P< 0.05$; $^{b}P< 0.01$; $^{c}P< 0.001$.

total fluxes of K, N, P, Ca, and Mg were 31, 27, 22, 19, and 12 % lower in MMor litterfall. The annual flux of Al in total PMull litterfall was more than three times the amount transferred in the MMor forest and over four times larger if only leaf fall is taken into consideration (Table 8.5).

Compared to amounts of nutrients present in the top 50 *cm* of the soil column (*cf.* Table 2.11 in Chapter 2), the nutrient fluxes in small litterfall ranged between <0.3 % for total P to >20 % for exchangeable Ca; for exchangeable K and Mg they were typically 10–16 % *vs.* 2.3 and 0.4 % for total N in the PMull and MMor, respectively (Table 8.6). Expressed against nutrient inputs to the forest floor via net precipitation (Table 7.4), nutrient fluxes in small litterfall were generally much higher except for K which must have been severely underestimated because of leaching from the littertraps (Table 8.5). The relative importance of litterfall was greater in the PMull for all elements (Table 8.6).

8.4.5 Foliar nutrient concentrations

For most elements, concentrations in PMull foliage were higher than those in the MMor, except for Mg and Al which were marginally higher in the MMor forest (Table 8.7). However, the contrasts were small and not significant. Concentrations of P, K, and polyphenols were considerably lower (*c.* 30–70 %) in leaf litterfall than in living crown leaves, but N was reduced by 10–15 %. Concentrations of Ca and Mg in leaf litter were increased compared to those in foliage, the increases for Ca being *c.* 40 % (MMor) to 50 % (PMull) *vs.* 6 % (MMor) to 20 % (PMull) for Mg. The most remarkable contrast emerged for Al as the concentrations in foliage (which were not significantly different between the PMull and the MMor) roughly doubled in leaf litter collected in the MMor, but increased ten times in leaf litter from the PMull forest (Table 8.7).

Table 8.5: Annual nutrient accession ($kg\,ha^{-1}\,yr^{-1}$; C in $t\,ha^{-1}\,yr^{-1}$) via leaf, wood, trash and total litterfall in the PMull and MMor forests.

Forest	Fraction	C	N	P	Ca	K	Mg	Al	Phenols
PMull	leaf	2.46^a	39.60^b	2.05^c	40.40^a	8.79^c	11.06	4.60^b	410
	trash	0.34^b	8.64^b	0.64^b	5.23^b	1.99^a	1.32^a	0.46^b	22
	wood	0.27	4.65	0.21	4.62	0.61	0.85	0.16	5
	total	3.08^a	52.90^b	2.89^c	50.24^a	11.39^c	13.23	5.22^b	437
MMor	leaf	2.24^a	28.16^b	1.54^c	31.85^a	6.20^c	9.79	1.04^b	471
	trash	0.22^b	5.19^b	0.44^b	3.75^b	1.11^a	0.96^a	0.26^b	15
	wood	0.44	5.20	0.26	4.89	0.55	0.85	0.20	9
	total	2.90^a	38.55^b	2.24^c	40.49^a	7.86^c	11.60	1.50^b	495

Significant differences per category (leaf, trash, wood or total) between forests (paired *t-test* for means; $n = 12$) are indicated by the same letter: ^{a}P< 0.05; ^{b}P< 0.01; ^{c}P< 0.001.

Table 8.6: Annual nutrient accession ($kg\,ha^{-1}\,yr^{-1}$; C in $t\,ha^{-1}\,yr^{-1}$) to the forest floor via total small litter fall *vs.* that via net precipitation compared to soil nutrient reserves in the top 50 *cm* ($kg\,ha^{-1}$; C in $t\,ha^{-1}$).

Forest	Fraction	N	P	Ca	Mg	K
PMull	Total litter fall LF	52.9	2.9	50.2	13.2	11.4
	Net precipitation NP	5.4*	0.18*	13.2	5.9	44.0†
	LF ÷ NP (%)	980	1600	380	225	26
MMor	Total litter fall LF	38.6	2.2	40.5	11.6	7.9
	Net precipitation NP	4.5*	0.18*	12.1	6.4	33.3†
	LF÷ NP (%)	860	1220	335	180	24

*mineral forms only; † seriously underestimated because of leaching from the littertraps.

Table 8.7: Mean nutrient concentrations ($mg\,g^{-1}$; standard deviations between parentheses) of foliage from eight principal tree species as collected in December 1994 in the PMull and MMor forests. Foliar concentrations per species were weighed according to their relative contributions to annual leaf litterfall. Phenol concentrations are expressed in $mg\,\mathrm{TAE}\,g^{-1}$. Litter data are from Table 8.4. Retranslocation (retrans.) is expressed as percentage of foliar concentrations (Eq. 8.2).

Forest	Fraction	N	P	Ca	K	Mg	Al	Phenols
PMull	foliage	8.6	0.64	5.2	4.9	1.8	0.09	171
		(3.2)	(0.27)	(3.1)	(2.3)	(1.2)	(0.04)	(39)
	litter	7.7	0.40	7.9	1.7	2.2	0.90	80
		(1.00)	(0.12)	(0.95)	(0.54)	(0.29)	(0.18)	(23)
	retrans. (%)	41	59	-	77	21	-560	69
MMor	foliage	7.2	0.53	5.0	4.3	2.0	0.10	162
		(1.8)	(0.11)	(2.8)	(1.5)	(1.2)	(0.03)	(34)
	litter	6.1	0.33	6.9	1.3	2.1	0.22	102
		(1.85)	(0.07)	(0.73)	(0.26)	(0.50)	(0.05)	(34)
	retrans. (%)	39	55	-	77	23	-60	54

In the absence of information on the seasonal variability of foliar chemistry, the degree of nutrient retranslocation before leaf abscission can be approximated if Ca is assumed to be immobile once located in foliar tissue [*Vitousek and Sanford*, 1986]. Relative retranslocation of a particular nutrient X is then evaluated as:

$$\frac{[x]_l \cdot \frac{[\mathrm{Ca}]_l}{[\mathrm{Ca}]_f} - [x]_f}{[x]_f} \times 100\% \qquad (8.2)$$

where $[\mathrm{Ca}]_{f,l}$ and $[\mathrm{X}]_{f,l}$ are the measured concentrations of Ca and element X in foliage and litter, respectively. Applying this method to the PMull and MMor forests gave surprisingly similar results: 40 % retranslocation for N and 77 % for K in both forests; 59 % and 55 % for P in the PMull and MMor, respectively, and 20–23 % for Mg. The high retranslocation values derived for K must be regarded as an artefact due to the leaching problem referred to earlier. However, contrasting results between the forests were obtained for polyphenols (69 % *vs.* 54 % 'retranslocation') and, especially, for Al (negative retranslocations of −560 % and −60 % in the PMull and MMor, respectively (Table 8.7)). As previously shown in Section 3.4.1, concentrations of Al in foliar tissue increased significantly with leaf age in both forests.

8.5 Discussion

8.5.1 Litterfall and climatic conditions

Rates of litterfall in this study may have been underestimated due to (i) weight loss prior to collection associated with leaching and initial decomposition in the traps, (ii) small particles passing the 1 *mm* mesh of the netting, (iii) interception of litter by the standing vegetation, especially bromeliads, and (iv) incomplete

sampling of litter generated by understorey vegetation [*cf. Proctor*, 1983; *Veneklaas*, 1990]. The associated total error is judged to be small, however. The dominant leaf fall fractions showed relatively low spatial variability (Table 8.1) and main canopy leaf litter, therefore, is considered to be sampled reasonably well. The prolonged residence time (maximum 3–4 weeks) of trapped material, however, should be taken into consideration. At the present localities, weight loss from litterbags placed on the forest floor reached 5–20 % during the first 50 days (Section 9.3.1). Although these rates of litter disappearance cannot be applied directly to trapped foliage (the above-ground position of litter includes full drainage and adequate ventilation and excludes most soil faunal activity and therefore lowers decomposition rates [*Kunkel and Kunkel*, 1979]), a 2–4 % underestimation of the present leaf fall rates due to decay prior to collection cannot be ruled out.

As in other tropical forests [*Vitousek and Sanford*, 1986] the present leaf fall rates showed considerable seasonal variation (Fig. 8.1). As noted also in an earlier study in several nearby forests by *Tanner* [1980a], leaf fall in the PMull and MMor forests was inversely related to rainfall distribution, *i.e.* high average rates of leaf fall coincided with low daily precipitation and *vice versa* (Fig. 8.2). Considering the observations made during April–June 1995 to be typical for overall dry season litterfall rates (2.70 and 2.46 $g\,m^{-2}\,d^{-1}$ in the PMull and MMor, respectively) and those for September–December to be typical for the wet season (0.77 and 0.56 $g\,m^{-2}\,d^{-1}$), quotients between dry- and wet season leaf fall production amount to 3.5 for the PMull and to 4.4 for the MMor forest. These correspond reasonably well with the ratio of average daily dry- to wet season rainfall (3.7). Absolute differences in leaf fall between the two seasons were identical for both forest types (1.9 $g\,m^{-2}\,d^{-1}$) but the higher ratio obtained for the MMor forest suggests a slightly enhanced sensitivity to drought compared to the PMull forest (see also below). *Tanner* [1980a] found an opposite pattern for litterfall over 1974–1975 and 1977–1978 in his Mull and Mor Ridge forests: there the corresponding ratios were rather smaller but this time the highest value (1.48) was obtained for the Mull Ridge forest *vs.* 1.29 for the Mor Ridge Forest (E. V. J. Tanner, *personal communication*, 1999). The contrast between the highest and lowest litter production (for 2 week collections), however, was highest in the Mor Ridge forest. In the present study, such differences in minimum-maximum litter production were absent (minimum 0.7 $g\,m^{-2}\,d^{-1}$; maximum 3.2 $g\,m^{-2}\,d^{-1}$ in both forests).

As for the relative sensitivity to drought of the different forest types in the study area, it was demonstrated in Section 2.3.3 that amounts of plant available water (PAW) in the top 50 *cm* of the respective soils exhibit a modest difference between Mor-type soils (PAW: 128–137 *mm*; average soil water content 0.26–0.27 $g\,cm^{-3}$) and Mull-type soils (PAW 166–190 *mm*; 0.33–0.38 $g\,cm^{-3}$) which agrees with the higher ratios of dry to wet season litterfall in the MMor forest noted earlier. However, monthly observations of gravimetric soil water contents throughout 1980 by *Kapos and Tanner* [1985] and of soil water tension ψ_m (at 3–4 day intervals) between January 1995 and April 1996 by the present study (Section 5.5.4) confirmed that soil water tensions never reached perma-

nent wilting point ($\psi_m < -1.58$ *MPa*; *Landsberg* [1986]) in any of the studied forests (Mull Ridge, Mor Ridge, PMull, MMor). Nevertheless, soil water tensions of -1000 *cm* (-0.1 *MPa*, beyond which water uptake is considered to fall below the potential rate; *Landsberg* [1986]) were approached occasionally in the MMor forest in 1995 (see Section 5.5.4 for details) but were frequently exceeded in 1980 [*Kapos and Tanner*, 1985]. Whilst the vegetation thus may have experienced mild water stress at times, the fact that the threshold value of -0.1 *MPa* was reached far more frequently in the taller-statured Mull-type forest than in stunted Mor forest [*Kapos and Tanner*, 1985] suggests that the degree of soil water stress cannot be held responsible for decreased forest stature. The contrasts in soil water patterns between the forests observed by *Kapos and Tanner* [1985] did parallel the difference in dry to wet season litterfall ratios between Mor and Mull-type forests as reported by *Tanner* [1980a] (*personal communication*, 1999). *Bruijnzeel et al.* [1993] also demonstrated that one of the severest droughts in the area's history caused significant extra shedding of leaves below but not within the cloud belt of a low coastal mountain in East Malaysia.

During 1995–1996, no occasional pulses of litterfall (*e.g.* due to strong winds [*Nadkarni and Matelson*, 1992b] or severe rain/hail storms [*Veneklaas*, 1990]) were observed in the study area. However, the quantification of such pulses would require litter to be collected at shorter intervals (<1 week, *Nadkarni and Matelson* [1992b]). Such data are not available for Jamaica's montane forests. Catastrophic forest disturbance, *e.g.* due to passing hurricanes, has been reported for Puerto Rico [*Scatena et al.*, 1993, 1996] and the study area [*Bellingham*, 1993] but the most recent hurricane passage (Hurricane Gilbert, September 1988) is probably too long ago (>7 years) to have a noticeable influence on, for example, leaf litter standing crop or post-hurricane synchronization of leaf life (and therefore litterfall patterns) [*McDonald*, 2000].

8.5.2 Comparison with other tropical montane forest sites

Total and leaf litterfall

The present amounts of total litterfall (6.2–6.5 $\cdot\, t\, ha^{-1}\, yr^{-1}$) are at the low end of the spectrum reported for montane rain forests in the wet tropics of South America and South East Asia (range: 5.6–11.0 $t\, ha^{-1}\, yr^{-1}$; Table 8.8) but generally higher than observed for (shorter-statured) mossy lower and upper montane forests (3.1–5.3 $t\, ha^{-1}\, yr^{-1}$). Comparisons between different studies are often difficult due to contrasts in methodology [*Proctor*, 1983, 1984]. For total and leaf litterfall the problem is relatively small but differences in methodology have more pronounced effects for the other fractions (*e.g.* the use of different diameter limits for woody litterfall; sampling procedures for trash etc.). Nevertheless, the present results illustrate the intermediate position of the Jamaican forests in the overall spectrum, both for total fine litterfall and leaf litterfall (Table 8.8). Also, the current total small litter production totals are very similar to those obtained by *Tanner* [1980a] for four ridge top forests in the study area (range: 5.5–6.6 $t\, ha^{-1}\, yr^{-1}$). For lower elevations in the Blue Mountains (*c.* 1300 *m* a.s.l.), litterfall is considerably

Table 8.8: Leaf-, miscellaneous, woody and total litterfall ($t\,ha^{-1}\,yr^{-1}$), leaf- and total litter standing crops ($t\,ha^{-1}$, LSC_l and LSC_{tot}) and decay constants for leaf- and total litter (k_L and k_{tot}) for selected wet tropical montane rain forests ($1400 > P < 5700\ mm$).

Location	Alt.	Forest	Leaf	Mis.	Wood	Total	Leaf	LSC_l	LSC_{tot}	k_L	k_{tot}
	m	type	$t\,ha^{-1}\,yr^{-1}$				perc.	$t\,ha^{-1}$	$t\,ha^{-1}$	-	-
Brunei, Bukit Belalong[1]	500	LRF	7.9	1.0	1.6	10.5	75	3.2	6.1	2.4	1.6
	850	LMRF	6.0	0.9	1.3	8.3	72	3.1	5.2	2.0	1.5
East Malaysia, Gunung Silam[2]	610	LMRF	4.1	0.6	0.9	5.6	73	3.9	-	1.06	-
	870*	LMRF	3.3	0.6	0.9	4.8	69	2.5	-	1.33	-
Indonesia, Central Java[3]	1000	LMRF									
Puerto Rico, Pico del Este[4]	1015*	ECF	2.5	0.4	0.3	3.10	79	2.5	4.3	1.11	0.71
Costa Rica, Monteverde[5]	1500	LMRF	4.8	1.8	0.9	7.5	69	7.2	10.1	0.67	0.74
Sarawak, Gunung Mulu[6]	1310	LMRF	5.7	2.1	3.2	11.0	52	-	-	-	-
	1860*	UMRF	2.3	0.7	0.6	3.6	64	-	-	-	-
Costa Rica, Volcán Barva[7]	1000	LMRF	5.5	-	1.1	6.6	83	2.4	4.2	2.31	1.57
	2000	LMRF	4.8	-	1.0	5.8	83	3.3	5.2	1.47	1.12
	2600	LMRF	4.6	-	0.7	5.3	87	3.7	6.3	1.24	0.84
Venezuela, San Eusebio[8]	2300	LMRF	3.4	1.1	2.3	7.0	49	-	38.0	-	0.18
New Guinea , Kerigomna[9]	2500	LMRF	6.5	-	0.9	7.4	84	6.1	7.1	1.07	1.04
Colombia, Central Cordillera[10]	2550	LMRF	4.6	1.1	1.0	7.0	66	-	-	-	-
	3370	UMRF	2.8	0.5	0.8	4.3	65	-	-	-	-
Jamaica, Green River[11a]	1300	LMRF	8.4	-	0.9	9.3	90	4.1	5.4	2.0	1.7
Jamaica, Green River[11b]	1300	LMRF	7.4	-	2.0	9.5	78	3.5	4.3	2.1	2.2
Jamaica, Mull[12]	1550	UMRF	5.3	-	0.2	5.5	96	11.7	-	0.44	-
Jamaica, PMull[13]	1809	UMRF	5.1	0.7	0.6	6.5	79	4.3	7.5	1.36	0.87
Jamaica, MMor[13]	1824*	UMRF	4.6	0.5	0.9	6.2	75	5.8	11.0	0.90	0.56
Jamaica, Mor[12]	1550*	UMRF	4.9	-	1.5	6.6	74	11.1	-	0.45	-

LRF: lowland rain forest; LMRF and UMRF: lower- and upper montane rain forest; ECF: elfin cloud forest; *stunted montane forests; [1] *Pendry and Proctor* [1996a]; [2] *Proctor et al.* [1989]; [3] *Weaver et al.* [1986]; [4] *Bruijnzeel* [1984]; [5] *Nadkarni and Matelson* [1992a, b]; [6] *Proctor et al.* [1983b]; [7] *Heaney and Proctor* [1989]; [8] *Steinhardt* [1979]; [9] *Edwards* [1977, 1982]; [10] *Veneklaas* [1990]; [11a] secondary forest, [11b] primary forest, *McDonald* [2000]; [12] *Tanner* [1980a, 1981]; [13] present study.

higher. *McDonald* [2000] recorded 7.2–9.9 $t\,ha^{-1}\,yr^{-1}$ of total small litterfall (90 % leaves) for primary and secondary forests on less acidic (pH>4.9) soils. The increasing contribution by the leaf fraction when going from stunted Mor forest to taller-statured Mull forest [*Tanner*, 1980a] are maintained when the present intermediate forest types are included. In other words, whilst absolute differences in leaf litterfall between the four forests are relatively small, the cycling of organic matter via leaf fall is reduced in the Mor-type forests (Table 8.8).

Woody litterfall
Due to its erratic distribution, inter-site contrasts for woody litter fall are large. The exceptionally high wood fall in the low elevation site at Gunung Mulu [*Proctor et al.*, 1983b] can probably be explained by the fact that only 16 weeks of data were extrapolated to a full year. The high wood fall for the site in Venezuela [*Steinhardt*, 1979] is believed to be caused by the inclusion of outlying data [*Veneklaas*, 1990]. Except for these examples, mean annual wood fall in montane forests amounts to *c.* 1.0 $t\,ha^{-1}$ (Table 8.8). Woody litterfall in the MMor-type forests in Jamaica was similar or above this average but distinctly lower in the (P)Mull forests (Table 8.8). At 0.2 $t\,ha^{-1}\,yr^{-1}$ wood fall in the Mull forest is even lower than in the extremely stunted 'elfin' cloud forest at Pico del Este, Puerto Rico, a forest type with a woody biomass only half that reported for the Mull Ridge [*Weaver et al.*, 1986; *Tanner*, 1980b]. An explanation for this underestimation is currently lacking although methodological differences are believed to be at least part of the explanation (*E. V. J. Tanner*; *personal communication* 1999).

Epiphytic litterfall
Relative rates of epiphyte litterfall in Jamaica's montane forests (2.7, 2,2, 0.9, and 0.1 % of total litter fall in, successively, the Mor Ridge, MMor, PMull, and Mull Ridge forests; *Tanner* [1980a], Table 8.1) reflect the relative magnitude of epiphyte biomass [*Tanner*, 1980b] and are inversely related to main canopy height [*cf. Tanner*, 1977a, Table 2.1]. Relative epiphyte fall in the Mor [*Tanner*, 1980a] and MMor forests (Table 8.1) were much higher than in the taller Mull-type forests which had epiphyte falls similar to those usually observed in lowland forest (*e.g.* 0.8 % in Cameroon; *Songwe et al.* [1988]). However, absolute amounts of epiphytic litterfall in the Mor forests were considerably smaller than reported for 'real' mossy cloud forest (*e.g.* 230 $kg\,ha^{-1}\,yr^{-1}$ (3.3 %) in Venezuela [*Steinhardt*, 1979]; 230 $kg\,ha^{-1}\,yr^{-1}$ (3–5.3 %) in Colombia, *Veneklaas* [1990]; or 500 $kg\,ha^{-1}\,yr^{-1}$ (7 % in Costa Rica's Monteverde forest, *Nadkarni and Matelson* [1992a]). The low values observed for epiphytic litterfall in the Jamaican forests, and their relatively low epiphytic biomass compared to those of the quoted Central and South American forests [*cf. Bruijnzeel and Proctor*, 1995] are in line with the relatively low amounts of cloud water trapped by the present forests [Section 4.4.2; *cf. Clark et al.*, 1998]. They may even raise the question as to what extent the Jamaican forests represent 'true' cloud forests (see *Stadtmüller* [1987] and *Hamilton et al.* [1995] for a discussion of the problems with cloud forest terminology and definition).

8.5.3 Litter standing crop and annual decay constants

Litter standing crop

Due to the subjective distinctions between various ectorganic horizons that have been used in different studies [*Burghouts et al.*, 1998], comparison of litter standing crop (LSC) data is difficult, even more so because the transitions between various ectorganic layers of montane soils are often unclear [*cf. Edwards*, 1977]. Despite such methodological problems, reported amounts of total LSC in tropical montane forests of widely different statures vary surprisingly little (Table 8.8). Leaving the excessive value of 38 $t\,ha^{-1}$ reported for a tall LMRF in Venezuela aside (as it probably reflects a high proportion of woody material), LSC_{tot} ranged from *c.* 4.3 $t\,ha^{-1}$ to 10–11 $t\,ha^{-1}$. Interestingly, both the two reported minimum values and the two maximum values were for forests of greatly different biomass: at the low end of the spectrum the tall LMRF on Volcán Barva *vs.* the stunted elfin forest in Puerto Rico (both at elevations of *c.* 1000 *m* a.s.l.) and at the top end of the spectrum the equally tall LMRF at Monteverde, Costa Rica (at 1500 *m* a.s.l.) *vs.* the Jamaican MMor forest (at 1824 *m* a.s.l.). A similar picture emerges for leaf litter standing crops (Table 8.8). Such observations make it difficult to generalize about the underlying causes of differences between locations. Compared to other montane forests the LSCs (for leaves and total fine litter) of the short-statured MMor forest are high but much lower than recorded for the ridge top forests of *Tanner* [1981] (Table 8.8). The resemblance between leaf LSC in the Mor forest and total LSC in the MMor (11.1 and 11.0 $t\,ha^{-1}$, respectively) suggests the value for the Mor plot to represent the standing crop of total- rather than leaf litter (plus trash) only. *Tanner* [1981] estimated that wood contributed less than 0.5 % to the total LSC in his plots, despite the fact that wood fall in the Mor and Mull forests was approximately 15% of the total litter production [*Tanner*, 1980a] which, given the slow decomposition of wood compared to decaying foliage, should result in considerable accumulation of woody material. The absolute amounts of woody litter (*i.e.* LSC_{tot} minus LSC_l) in the PMull and MMor forests are high compared to those reported for other montane localities (Table 8.8). It is possible that the high absolute amounts of woody litter in the Jamaican forests reflect the effects of former hurricane disturbance [*cf. Scatena et al.*, 1996], although relative contributions of woody material (42 and 48 % of total LSC in the PMull and MMor, respectively) compare well with results for other montane forests (generally 36–48 %, Table 8.8).

Decay constants

Decomposition of organic material is a complex function of resource quality and quantity, environmental conditions and functioning of the decomposer community [*Burghouts*, 1993]. Slow decomposition in montane forests compared to lowland sites therefore has been attributed to, *inter alia*, lower temperatures, persistent wetness or the absence of wetting and drying cycles, and poor substrate quality (notably low nitrogen concentrations and high concentrations of phenolic compounds [*Grubb*, 1977; *Tanner*, 1981; *Edwards*, 1982; *Marrs et al.*,

1988; *Bruijnzeel et al.*, 1993].

Reported annual decay constants for leaf material range from *c.* 0.45 in the Mor and Mull forests of the study area [*Tanner*, 1980a, 1981] to 2–2.4 for tall-statured LMRF at relatively low elevations in Costa Rica and Brunei [*Heaney and Proctor*, 1989; *Pendry and Proctor*, 1996a]. Most values, however, are reasonably close to 1.0 (±0.35), regardless of forest type and stature. The very low k_L values derived for the nearby Mor and Mull Ridge forests by *Tanner* [1981] primarily reflect the high LSCs that were commented upon already. The k_L <0.5 (suggesting considerable accumulation of organic matter) is certainly not in agreement with field observations for Mull-type ectorganic layers in the study area [*Spijkerman*, 1996, *cf.* Appendix A]. Further support for this contention comes from the fact that the LSC_l of the PMull forest (4.3 $t\,ha^{-1}$) was very similar to the 4.1 $t\,ha^{-1}$ reported for nearby secondary LMRF at 1300 *m* a.s.l. and higher than the 3.5 $t\,ha^{-1}$ in primary forest at that elevation [*McDonald*, 2000]. Standing crops of woody litter in the latter two forests (1.2 and 0.9 $t\,ha^{-1}$, respectively) were distinctly lower than the 3.1–5.2 $t\,ha^{-1}$ of the PMull and MMor forest plots, possibly reflecting differences in site exposure to high winds [*McDonald*, 2000].

Decay constants generally decrease with elevation on single mountains (*e.g.* Volcán Barva, Costa Rica; Bukit Belalong, Brunei) and the Jamaican data (1300 *vs.* 1815 *m* a.s.l.) confirm this (Table 8.8). The decay constant for total fine litter (k_{tot}) derived for the MMor forest (and to a lesser extent for PMull forest as well) ranks as the lowest reported for any montane tropical forest (if the exceptionally low value of 0.18 reported for a tall LMRF in Venezuela [*Steinhardt*, 1979] is not included). Because the present data on LSC_l include a small amount of non-leaf material (notably seeds), which is more recalcitrant to decomposition, it is possible that the estimated k_L values for the PMull and MMor forest have been underestimated slightly. Similarly low k_{tot} values have been described for both tall (Volcán Barva at 2600 *m* a.s.l., *Heaney and Proctor* [1989] ; Monteverde, *Nadkarni and Matelson* [1992a, b]) and extremely stunted (Puerto Rico; *Weaver et al.* [1986]) montane forests elsewhere. Whilst the latter forests all have wet to very wet climatic conditions in common [*Marrs et al.*, 1988; *Clark et al.*, 1998; *Weaver et al.*, 1986], excess wetness cannot be the primary factor causing low k_{tot} in the Jamaican forests (*cf.* Section 5.6.4). Also, climatic factors alone cannot explain the contrasts in decay constants between the PMull and MMor forest (43–51 % higher in the PMull; Table 8.8). Litter quality must also play an important role (see below).

8.5.4 Nutrient concentrations

Nutrient concentrations in leaf litterfall from a range of montane forests in the wet tropics are listed in Table 8.9 but, as noted earlier for litterfall amounts, comparisons between studies suffer from differences in fraction definition, collection procedures and analytical techniques [*Proctor*, 1983]. The presently found concentrations of P in leaf fall in the PMull and MMor forests, for example, are much higher than those for the nearby Mull and Mor Ridge forests

by *Tanner* [1977b]. Differences in analytical techniques (vanadomolybdate-yellow method *vs.* ICP emission) and sample digestion (nitric/perchloric acid *vs.* micro-wave digestion in nitric/hydrocloric acid) are probably part of the explanation for such differences. Compared to montane sites elsewhere, P concentrations in leaf fall were intermediate in the PMull forest and on the low side in the MMor forest (Table 8.9).

Many of the sites listed in Table 8.9 are on moderately fertile volcanic substrates and concentrations of P, Ca, and Mg are usually higher there than in the leaf fall associated with forests on more leached sedimentary substrates (*e.g.* Brunei, Sarawak). Concentrations of Mg in leaf litter in the Jamaican forests are comparable to those found elsewhere whereas concentrations of Ca assume an intermediate position (higher in forests on fertile young volcanics and lower for sedimentary sites). Concentrations of K are affected too much by leaching from the collection traps to allow meaningful generalizations but the concentrations in leaf fall in the PMull and MMor are comparable to those obtained for very stunted forest in Puerto Rico and Sarawak (Table 8.9). Assessing the amount of leaching between leaf abscission and collection of the litter is difficult.. However, if it is assumed that all K will be leached from the litter within one year, the discrepancy between K fluxes in litter percolate and net precipitation (64.7 and 35.0 $kg\,ha^{-1}\,yr^{-1}$ in the PMull and MMor, respectively; Table 7.5) may be used as a rough approximation of the total annual amount of K delivered to the forest floor via litterfall. Thus, K in litterfall in the PMull and MMor forest may amount to *c.* 65 and 35 $kg\,ha^{-1}$ respectively, suggesting 53 and 27 $kg\,ha^{-1}\,yr^{-1}$ of K were leached from the littertraps prior to collection. However, given the amounts of total small litterfall (6.47 $t\,ha^{-1}\,yr^{-1}$ in the PMull and 6.16 $t\,ha^{-1}\,yr^{-1}$in the MMor forest), these leaching figures would imply original average K concentrations in small litterfall of prior to abscission amount to to 10 and 5.7 $mg\,g^{-1}$ for PMull and MMor litter, respectively, *i.e.* 2 and 1.3 times the average K concentrations in fresh foliage (Table 8.7). Clearly, the true transfer of K in small litterfall in the study forests lies somewhere between these extremes.

Concentrations of N in leaf litter from the Jamaican Mor-type forests are among the lowest reported for any tropical montane forest (Table 8.9) and similar to the ones found in heath forest on nutrient-deficient Podzols (Spodosols) in the Amazon (6–7 $mg\,g^{-1}$; *Cuevas and Medina* [1986], *Brouwer* [1996]).

On single mountains, a distinct inverse relationship between nutrient concentration and altitude is usually recognized for N and Ca, and to a lesser extent K, but not for P and Mg [*Bruijnzeel and Proctor*, 1995; *Tanner et al.*, 1998]. The Jamaican ridge top forests are not subject to major elevational contrasts, but they do show increasing concentrations of N and Ca in leaf litterfall with increasing stature (Table 8.9).

Lack of comparative information makes it difficult to put the concentrations of Al found in the leaf litter of the PMull and MMor forests in perspective. However, *Steinhardt* [1979] reported a concentration of 1.83 $mg\,g^{-1}$ in the leaf litter of a tall LMRF on sedimentary rock in Venezuela whereas *Bruijnzeel* [1984] obtained a value of 0.71 $mg\,g^{-1}$ for an equally tall-statured MRF (but non-cloud

forest) on volcanic soil in Central Java, Indonesia. Compared to these limited data, the 0.9 $mg\,g^{-1}$ found in leaf litter in the PMull forest falls within the reported range but that for the MMor is distinctly lower. Concentrations of Al in the litter percolate in the Venezuelan and Jamaican forests also decrease in the order Venezuela>PMull>MMor (Table 2.15). However, no such sequence exists for Al concentrations in topsoil moisture. As discussed in more detail in Chapter 2 (Table 2.15) and Section 7.4.3 (Table 7.4), Al concentrations in moisture extracted from the Ah-horizon of the MMor forest ($c.\,43$ $\mu mol\,l^{-1}$) were about twice those in the PMull ($c.\,21$ $\mu mol\,l^{-1}$) but lower than in the Venezuelan topsoil ($c.\,61$ $\mu mol\,l^{-1}$). Also, weighted mean foliar concentrations of Al did not differ significantly between the PMull and the MMor forest (Table 8.7). Laboratory experiments using seedlings of principal tree species grown in soil solutions with different concentrations of Al and pH would be helpful in investigating this issue further.

Concentrations of polyphenols in leaf litter from the PMull and the MMor forests differed not as much as might be expected on the basis of the observed contrasts in soil pH [*Northup et al.*, 1995] and foliar N [*Horner et al.*, 1988; *Bruijnzeel et al.*, 1993]. Generally, at sites with Mor humus formation higher amounts of phenols are seen to accumulate in plant tissue whereas species growing on Mull-type soils tend to have lower phenol concentrations [*Coulson et al.*, 1960; *Davies*, 1971; *Kuiters*, 1990]. Phenol concentrations in PMull leaf litter were only marginally lower than in MMor litter (80 *vs.* 102 $mg\,\mathrm{TAE}\,g^{-1}$; Table 8.7). Again, there are few comparative data to put these results in perspective. *Bruijnzeel et al.* [1993] suggested the existence of a negative correlation between concentrations of phenols and total N in leaf litter (Fig. 8.5). For example, litter from stunted forest on Mount Gedeh (Java) showed a decrease in N and an increase in phenol concentration compared to non-stunted forest at lower elevations whereas litter along the elevational gradient on Bukit Belalong, Brunei (where no cloud cap or stunted forest are found; *Pendry and Proctor* [1996b]), did not show such a trend. Interestingly, two fresh litter samples from Tanner's Mor and WMull forest plots (which were analyzed for phenols by *Bruijnzeel et al.* [1993]) showed (much) higher phenol concentrations for corresponding levels of N compared to material from other sites (Fig. 8.5). Also the concentration of phenols in leaf litter from the Mor forest was markedly higher than for the WMull (Fig. 8.5, *cf.* Table 8.9). Because the present data set cannot be compared directly with these single samples of litter on the forest floor further work on the phenolic contents of leaf fall in Mor and Mull-type forests and other tropical montane forests would be desirable. However, the presently obtained concentrations in leaf litter from the PMull and MMor suggest that they are elevated compared to results found elsewhere (Fig. 8.5; *Bruijnzeel et al.* [1993]). As such, although N concentrations in leaf litterfall in the PMull and MMor are low (Table 8.9), it is likely that factor(s) other than N limitation alone are at work in the Jamaican situation.

A comparison of nutrient concentrations in leaf litterfall (Table 8.4) and living foliage (Table 8.7) is often made to assess the degree of nutrient retranslocation before leaf abscission [*Vitousek*, 1984]. The present foliar data should

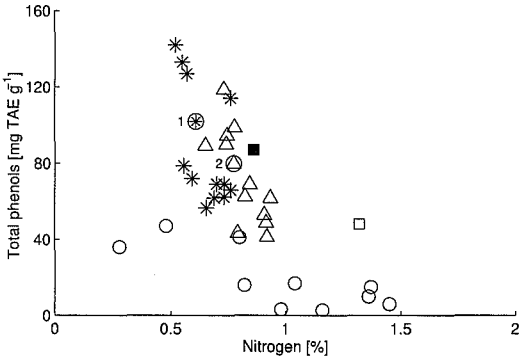

Figure 8.5: Concentrations of total nitrogen (%) and total phenols ($mg\,\mathrm{TAE}\,g^{-1}$) in fresh leaf litter from wet tropical mountains. ○ data from *Bruijnzeel et al.* [1993]; ■ Mor Ridge litter, □ WMull Ridge litter [*Bruijnzeel et al.*, 1993]. ∗ MMor litterfall, [1]plot average; △ PMull litterfall, [2]plot average (present study, 12 collections).

be viewed with caution, however, because they are based on a single collection in time (December 1994) which ignores potentially important temporal variations in foliar chemistry. Indeed, additional samples taken in April 1997 from the same tree species had showed lower concentrations of Ca and (especially) K, similar Al and Mg levels but higher P concentrations (see Section 3.4.1 for details).

Also, whilst foliar concentrations of P in nearby tall Mull forest and stunted Mor forest as determined by *Tanner* [1977a] on samples taken in March 1975 were similar to the presently found values, concentrations of Ca, K, and Mg, and especially N were all distinctly higher. Similarly, *Nadkarni and Matelson* [1992b] reported large seasonal fluctuations in foliar chemistry for cloud forest at Monteverde, Costa Rica. Concentrations of N and P were approximately 40 % higher in the dry- compared to the wet season whereas K concentrations decreased by 80 % in the dry season. Finally, mean foliar concentrations of Ca in that study were 25 % below the average concentration in leaf litter [*Nadkarni and Matelson*, 1992b]. The reported degree of retranslocation of N and P in montane forests varies widely. Between 25 and 48 % of N has been found to be retranslocated and between 25 and 69 % of P [*Bruijnzeel and Proctor*, 1995]. Taking the concentrations given in Tables 8.4 and 8.7 at face value, 38 % of P was retranslocated in both the PMull and MMor forests. Corresponding results for N were 13 % (PMull) and 15 % (MMor). Concentrations of Ca in the leaf litter of the PMull and the MMor forests exceeded those in living foliage by 51 % and 38 %, respectively. Although the disappearance of organic material from the traps may have increased Ca concentrations in leaf fall somewhat, the observed increases were too high to be explained in this way. A combination of seasonal variation in foliar chemistry [*Nadkarni and Matelson*, 1992b] and residual enrichment of Ca concentrations because of the large leaching losses inferred for K from the trapped material (Section 8.4.3) constitute an explanation. *Tan-*

Table 8.9: Concentrations ($mg\,g^{-1}$ dry weight) of nutrients in leaf litterfall in selected montane forests in the wet tropics. Phenol concentrations are expressed in $mg\,\mathrm{TAE}\,g^{-1}$.

Location	Alt.	Forest	N	P	Ca	K	Mg	Al	Phenols
	m	type				$mg\,g^{-1}$			
Brunei, Bukit Belalong	850	LMRF	11.3	0.32	2.1	4.9	2.5	-	15
East Malaysia, Gunung Silam	610	MRF	10.5	0.17	10.7	2.6	4.8	-	16
	870	LMRF	8.3	0.20	5.8	0.9	3.0	-	41
Indonesia, Central Java	1000	LMRF	11.2	0.55	21.6	4.8	3.9	0.74	-
Puerto Rico, Pico del Este	1015	ECF	7.7	0.24	5.3	1.4	4.4	-	-
Costa Rica, Monteverde	1500	LMRF	14.7	0.80	19.1	1.2	2.7	-	-
Sarawak, Gunung Mulu	1310	LMRF	8.1	0.21	1.9	3.7	1.8	-	0.02†
	1860	UMRF	7.4	0.26	1.9	1.8	2.0	-	0.02†
Costa Rica, Volcán Barva	1000	LMRF	11.0	0.45	7.2	1.4	1.9	-	-
	2000	LMRF	9.0	0.54	11.0	2.2	1.9	-	-
	2600	LMRF	6.8	0.53	10.4	3.0	2.3	-	-
Venezuela, San Eusebio	2300	LMRF	11.8	0.62	7.3	5.7	2.6	1.83	-
New Guinea, Mt. Kerigomna	2500	LMRF	11.5	0.60	12.4	5.2	2.8	-	-
Colombia, Cordillera Central	2550	LMRF	11.1	0.74	-	8.9	-	-	-
	3370	UMRF	7.8	0.40	-	3.5	-	-	-
Jamaica, Green River[2]	1300	LMRF	9.2	0.95	-	-	-	-	-
Jamaica, Mull[1]	1550	UMRF	8.4	0.25	9.1	5.9	3.2	-	48*
Jamaica, PMull	1809	UMRF	7.7	0.40	7.9	1.7	2.2	0.90	80
Jamaica, MMor	1824	UMRF	6.1	0.33	6.9	1.3	2.1	0.22	102
Jamaica, Mor[1]	1550	UMRF	6.0	0.18	5.8	2.3	3.3	-	87*

References as in Table 8.8 except for Jamaican Mor and Mull forests. [1] *Tanner* [1977b]; [2]Values for total fine litterfall in secondary forest only [*McDonald*, 2000]; * *Bruijnzeel et al.* [1993]. †Phenol concentrations underestimated due to leaching from littertraps (residence time >4 weeks) and evaporation during drying of samples at 105 °C.

ner [1977b] calculated 54 and 49 % retranslocation of N and 62 and 31 % of P in tall Mull and stunted Mor forest, respectively. Normalization of the nutrient concentrations in leaf fall in the PMull and MMor for Ca and re-computing the low retranslocation rates cited earlier for the two forests estimates of 41 % and 39 % for N and 59 % and 55 % for P in the PMull and MMor, respectively, which are more in line with values obtained for other montane forests [*Bruijnzeel and Proctor*, 1995].

8.5.5 Nutrient fluxes via litterfall

The nutrient fluxes via litterfall were all higher in the PMull forest compared to the MMor (Table 8.5). The largest contrasts were observed for N and K (both *c.* 30 %) and for P and Ca (20 %). Compared to lower montane rain forests elsewhere in the world, the annual accession of N via total fine litterfall in the Jamaican forests is very low, especially in the Mor-type forests, but comparable or higher than results derived for other upper montane rain forests (Table 8.10) and N-stressed heath forests on white sands in Amazonia [*Herrera*, 1979; *Cuevas and Medina*, 1986] and Sarawak [*Proctor et al.*, 1983a]. Concentrations and

Table 8.10: Totals annual fine litterfall ($t\,ha^{-1}\,yr^{-1}$; including small wood, epiphytes, trash, and reproductive parts) and associated nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in selected montane forests in the wet tropics.

Location	Alt.	Forest	Litterfall	N	P	Ca	K	Mg
	m	type			$kg\,ha^{-1}\,yr^{-1}$			
Brunei, Belalong	850	LMRF	8.3	93	2.9	17	37	18
Sabah, Silam	610	LMRF	5.6	60.2	1.2	58.8	12.5	24.1
	870	LMRF	4.8	41.5	1.1	27.3	4.9	12.6
Indonesia, Central Java	1000	LMRF	7.4	75	3.7	144	35	25
Puerto Rico, Pico del Este	1015	ECF	3.1	23.9	0.7	16.3	4.6	7.6
Costa Rica, Monteverde	1500	LMRF	7.5	100.5	6.5	119.2	12.1	15.8
Sarawak, Mulu	1310	LMRF	11.0	86.1	2.5	20.6	31.4	16.2
	1860	UMRF	3.6	28.9	1.1	6.7	5.7	6.3
Costa Rica, Volcán Barva	1000	LMRF	6.6	65.9	2.6	44.7	8.7	11.8
	2000	LMRF	5.8	46.6	2.7	61.1	11.9	10.3
	2600	LMRF	5.3	33.8	2.6	51.8	15.4	11.4
Venezuela, San Eusebio	2300	LMRF	7.0	69.1	4.0	43.1	33.1	14.4
New Guinea, Kerigomna*	2500	LMRF	7.4	90.5	5.2	87.5	31.1	18.3
Colombia,	2550	LMRF	7.0	81.9	6.1	-	59.3	-
Cordillera Central	3370	UMRF	4.3	34.2	1.9	-	13.9	-
Jamaica, Green River[2]	1300	LMRF	9.3	80.8	7.73	-	-	-
Jamaica, Mull[1]	1550	UMRF	5.5	48.5	1.8	49.3	33.0	16.9
Jamaica, PMull	1809	UMRF	6.5	52.9	2.9	50.2	11.4	13.2
Jamaica, MMor	1824	UMRF	6.2	38.6	2.2	40.5	7.9	11.6
Jamaica, Mor[1]	1550	UMRF	6.6	39.5	1.5	32.5	14.1	18.2

References as in Table 8.8. [1]Values for Jamaican Mor and Mull forest calculated using concentrations from *Tanner* [1977b] and litterfall amounts from *Tanner* [1980a]; [2]values for secondary forest only [*McDonald*, 2000]. *Data for 'ridgetop' forest only [*Edwards*, 1977, 1982].

transfers of P, Ca, Mg and K in the Jamaican forests were generally intermediate between those observed for stunted UMRF and tall LMRF on fertile volcanic soils (Tables 8.9 and 8.10). Nutrient fluxes associated with epiphyte fall were not determined separately in the present study. Element transfers via epiphyte fall in very mossy cloud forests may constitute 1–8 % of total annual nutrient accession (typically 7 % for N and P; *Veneklaas* [1990], *Nadkarni and Matelson* [1992a]). However, given the much lower epiphyte fall determined for the present forests (Table 8.1), the associated nutrient fluxes are believed to be negligibly small [*cf. Bruijnzeel and Proctor*, 1995].

8.6 Conclusions

Despite the considerable physiognomic contrast between the taller-statured PMull and the stunted MMor forest (including a 20 % difference in leaf area index), the total inputs of small litter to the forest floor in the two forests were comparable at 6.5 and 6.2 $t\,ha^{-1}\,yr^{-1}$, respectively, as were the relative contributions percentages of leaf fall to total litterfall (79 % and 75 %). The inferred rates of litter decomposition was lower in the MMor forest: the mean standing

Table 8.11: Annual leaf litterfall ($t\,ha^{-1}\,yr^{-1}$) and associated nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in selected montane forests in the wet tropics.

Location	Alt.	Forest	Leaf fall	N	P	Ca	K	Mg
	m	type			$kg\,ha^{-1}\,yr^{-1}$			
Brunei, Belalong	850	LMRF	6.0	67.8	1.92	12.6	29.1	15.0
Sabah, Silam	610	LMRF	4.1	43.4	0.70	49.2	10.7	19.8
	850	LMRF	3.3	27.6	0.66	19.3	3.0	10.0
Puerto Rico, Pico del Este	1000	ECF	2.4	18.8	0.59	12.9	3.4	6.0
Costa Rica, Monteverde	1500	LMRF	4.8	70.0	3.80	90.9	5.7	12.9
Sarawak, Mulu	1310	LMRF	5.7	46.3	1.20	10.8	20.9	10.1
	1860	UMRF	2.3	17.0	0.60	4.3	4.0	4.6
Costa Rica, Volcán Barva	1000	LMRF	5.5	60.5	2.48	39.6	7.7	10.5
	2000	LMRF	4.8	43.2	2.59	52.8	10.6	9.1
	2600	LMRF	4.6	31.3	2.44	47.8	13.8	10.6
Venezuela, San Eusebio	2300	LMRF	3.4	39.0	2.10	24.8	19.4	8.8
New Guinea, Kerigomna*	2500	LMRF	6.2	71.7	3.74	77.4	32.4	17.5
Colombia,	2550	LMRF	4.6	51.3	3.39	-	41.0	-
Cordillera Central	3370	UMRF	2.8	22.0	1.11	-	9.8	-
Jamaica, Mull	1550	UMRF	5.3	47.0	1.73	47.2	32.5	16.5
Jamaica, PMull	1809	UMRF	5.1	39.6	2.05	40.4	8.8	11.1
Jamaica, MMor	1824	UMRF	4.6	28.2	1.54	31.9	6.2	9.79
Jamaica, Mor	1550	UMRF	4.9	31.3	1.22	26.9	12.0	15.7

References as in Table 8.8. Values for Jamaican Mor and Mull forest were calculated using concentrations from *Tanner* [1977b] and leaf fall amounts from *Tanner* [1980a]. *Nutrient accession for New Guinea calculated from leaf fall (approximately 96 % of total non-woody litterfall, *Edwards* [1977]) and chemical concentration data for 'ridge top' forest only [*Edwards*, 1982].

stocks of fine litter were estimated at 11.0 $t\,ha^{-1}$ for the MMor forest *vs.* 7.5 $t\,ha^{-1}$ for the PMull, giving annual decay constants for total fine litter of 0.59 and 0.87, respectively, and for leaf litter of 0.9 and 1.4. These relatively low decay constants (especially for the MMor) cannot be explained by excessive wetness of the soil and litter substrate (*cf.* Section 5.6.4). Neither can differences in (micro-) climatic factors explain the difference in decomposition between the two sites (*cf.* Chapter 4), suggesting that litter quality plays a dominant role.

Concentrations of N, P, Ca and K were all significantly lower (by *c.* 20 %) in leaf litterfall in the MMor forest compared to the PMull. Concentrations of Mg, Ca and K in leaf litter were moderate but N was very low compared to values for other tropical montane forests. The concentrations of phenols (which are believed to decrease the decomposability of organic matter) were 30 % higher (not significant) in MMor-type leaf litter but concentrations of Al in PMull leaf litter were four times those in MMor leaf litterfall (the difference was highly significant). These contrasts were reduced in the other litterfall fractions but concentrations of key elements in wood litterfall were, again, larger in the PMull.

The annual nutrient accession rates via total small litterfall for major nutrients were found to be 8 to 30 % lower in the stunted MMor forest compared to those in the taller-statured PMull: 39 *vs.* 53 $kg\,ha^{-1}\,yr^{-1}$ for N; 2 *vs.* 3 $kg\,ha^{-1}\,yr^{-1}$ for P; 40 and 50 for Ca, 8 and 11 for K; 12 and 13 $kg\,ha^{-1}\,yr^{-1}$ for Mg. Compared to montane forests elsewhere, the N and K fluxes via litterfall were low; those of P, Ca, and Mg moderate to high but all were high compared to annual nutrient accession observed in very stunted cloud forest. It is tempting to relate the smaller amounts of key nutrients (particularly N) that are cycled via small litterfall in the MMor forest (Table 8.5) and the slower rate at which these nutrients come available to plants to its lower stature [*cf.* *Tanner et al.*, 1998]. However, to complete the picture comparative information on litter mineralization and decomposition rates in the two contrasting forests is required, which will be presented in part III of this series (Chapter 9).

The contrasting concentrations of H^+ and Al^{3+} in topsoil moisture in the two forests (both much higher in the Mor-type forest; Table 2.12 and Fig. 2.9) suggest that acidity and levels of potentially toxic 'free' Al may play an important role in determining the observed contrasts in litter chemistry and decomposition patterns. Although concentrations of Al in living foliage differed little between the two forests, concentrations in PMull leaf litterfall were four times those found in the MMor forest, giving a corresponding difference in Al fluxes via litterfall. It would seem as though the better developed PMull forest disposes excess Al by first concentrating Al in foliar tissue prior to leaf abscission. The MMor forest seems unable to achieve this, for reasons that are as yet unclear. The increased phenolic concentrations in leaf fall in the MMor are probably related to the pH-Al induced stress and are believed to have multiple effects which will be examined further in part III of this series.

9

NUTRIENT DYNAMICS IN TWO UPPER MONTANE RAIN FORESTS OF CONTRASTING STATURE IN THE BLUE MOUNTAINS, JAMAICA. III. DECOMPOSITION, MINERALIZATION AND SOIL RESPIRATION*

ABSTRACT

To investigate nutrient mobilization from litter in two upper montane forests of contrasting stature at c. 1820 m a.s.l.in the Blue Mountains, Jamaica, the rates of decomposition, nitrogen mineralization and nitrification and soil respiration were determined. The variables used for monitoring the decomposition process were weight loss, carbon and nitrogen concentrations and dehydrogenase activity in leaf litter. Litterbags containing fresh leaves of three principal species were randomly distributed on the forest floor. After 58 weeks, the average mass loss was 56.4 % in the taller vs. *32.4 % in the stunted forest, with corresponding decay constants of 0.75 and 0.35* yr^{-1}, *respectively. During the 58 weeks, N concentrations in the decomposing substrate increased by 30–40 % and 50–55 % in the shorter- and taller-statured forest, respectively, but leaf litter from* Clethra occidentalis *showed a decrease of 23 %. Concentrations of KCl-extractable* NH_4*-N in the top 10 cm of the forest floor were higher in the stunted site; but initial concentrations of nitrate-N, net production of* NO_3*-N and net N-mineralization were all higher in the ectorganic layer of the taller-statured forest: viz. 10.6* vs. *6.2* $\mu g\, g^{-1}$; *30.5* vs. *4.3* $kg\, ha^{-1}\, yr^{-1}$ *and 642* $kg\, ha^{-1}\, yr^{-1}$ vs. −8.4 $kg\, ha^{-1}\, yr^{-1}$. *The total of nutrient inputs to the forest floor via net precipitation (Part I in this series; Chapter 7), small litterfall (Part II; Chapter 8) and N-mineralization (this chapter) proved sufficient to balance the estimated gross uptake for all key elements except for N (by 12 %) in the short-statured forest. However, application of the above-mentioned litterbag-based decay constants to general annual nutrient inputs via*

*With R. Hogervorst, L. A. Bruijnzeel and H. A. Verhoef. A slightly modified version of this chapter (Part III in a series of three) will be submitted to the *Journal of Ecology*.

small litterfall resulted in a P-deficiency in the taller-statured forest of about 20 % and in a more general nutrient limitation in the short-statured forest (Mg 12 % deficient, P 29 %, Ca 36 %, and N 75 %). The discrepancy between estimated amounts of available and required N arguably constitutes the most direct line of evidence for N-deficiency in the short-statured forest.

Densities of bacteria and soil respiration rates (CO_2) were higher in litter substrate in the taller forest but the contrast between was less well-pronounced for the fungal biomass and dehydrogenase activity. The higher density and activity of bacteria, the higher density of fungi, and the higher density and diversity of fungivores and predators in the organic layer of the taller-statured forest all suggest better biotically controlled decomposition (and nutrient mobilization) compared to that in the short-statured forest. Because the meteorological conditions in the, almost adjacent, forests were very similar. The retarded decomposition of organic matter in the latter forest type is believed to be primarily influenced by contrasts in chemical composition (mainly lower N and higher polyphenols) and increased acidity in its ectorganic horizons and topsoil.

9.1 INTRODUCTION

This paper constitutes the third and last of three papers on the nutrient dynamics of two upper montane rain forests of contrasting stature at *c.* 1820 *m* a.s.l. in the Blue Mountains of Jamaica. The taller of the two forests was classified as 'Poorly-developed' Mull forest (PMull) and the shorter as 'Moderately-developed' Mor forest (MMor). The two forests represent intermediate stages in a sequence of forest types with increasingly acid and humus topsoil and a gradual reduction in forest stature from so-called 'Well-developed' Mull forest (canopy height 12–17 *m*) to stunted Mor forest (canopy height 5–7 *m*) as identified by *Tanner* [1977a, 1980b]. A detailed description of the physiognomy, floristics and soils (including biotics) of the two forests has been given in Chapter 2.

In part I (Chapter 7) it was demonstrated that the soils underlying the two contrasting forest types generally showed a net accumulation of nutrients although the rate at which this occurred was smaller in the more stunted forest. Also, overall ecosystem nutrient losses via drainage were more than compensated for by atmospheric nutrient inputs (bulk precipitation plus cloud water), with the exception of Mg (both forests) and possibly K in the PMull forest. Furthermore, it was shown that the atmospheric nutrient inputs far exceeded net uptake rates associated with stem biomass increment, whereas amounts of readily available nutrients in water percolating through the litter layer equalled or exceeded corresponding rates of gross uptake (defined as net uptake plus nutrients in small litterfall) for Ca, Mg and K, but not for N and P. In part II amounts of nutrients cycled via (small) litterfall were shown to be typically 20–30 % lower in the more stunted MMor forest compared to the PMull, despite the fact that amounts of litterfall were not significantly different (6.2 *vs.* 6.5 $t\,ha^{-1}\,yr^{-1}$, respectively). Amounts of small litter on the forest floor also differed between the two forests, viz. 7.5 $t\,ha^{-1}$ in the PMull and 11.0 $t\,ha^{-1}$

in the MMor forest, suggesting overall annual decay constants based on $k_L = LF/\text{LSC}$ [*Anderson and Swift*, 1983] of 0.86 and 0.56, respectively, for total fine litter and 1.36 and 0.9 for leaf litter only.

In ecosystems on poor soils the major pathway for nutrient cycling, especially nitrogen and phosphorus, is the recycling through decomposition of detritus, dead plant material and microbial and animal residues [*Proctor*, 1987; *Berg et al.*, 1998]. Element mobilization by decomposition, therefore, relates directly to rates of nutrient cycling, soil development, maintenance of soil fertility and nutrient uptake ability, especially when soils have low intrinsic nutrient content, are highly acid, or severely leached [*Anderson*, 1988; *Spain*, 1984]. In other words, systems with low rates of decay tend to have lower productivity whereas in forests with rapid nutrient turn-over, primary productivity is relatively high and often irrespective of nutrient availability in the mineral soil below [*Scott et al.*, 1992].

In Chapter 2 it was hypothesized that the observed contrasts in stature between Mor- and Mull-type forests in the study area could be explained in terms of differences in concentrations of H^+ (acidity) and potentially toxic 'free' aluminium (Al^{3+}) in the soil solution which might not only hamper the forests nutrient uptake capacity but also induce high foliar concentrations of polyphenols in the more stunted Mor-type forests [*Northup et al.*, 1995]. These, in turn, would affect the breakdown of litter, the release of nitrogen, and the detoxification of excess aluminium. Phenol concentrations in MMor leaf litter were 25–30 % higher than in the PMull, whereas N was *c.* 20 % lower (Table 8.4). Conversely, leaf litter in the PMull had four times more Al than MMor leaf litter.

The present chapter examines the patterns and rates of leaf litter disappearance, microbial activity, soil respiration, and N-mineralization and nitrification in the two study forests.

9.2 Materials and methods

9.2.1 Study sites

A detailed description of the structural and floristic characteristics of the PMull and MMor forests has been given in Chapter 2, along with a discussion of the physical and chemical characteristics of the soils (including biotics). A summary description was provided in part I of this series.

As for the climatic elements that affect decomposition, rainfall is unevenly distributed over the year and inter-annual differences are considerable. October and November are usually very wet (>350 *mm* each) with a secondary rainfall peak in May and June. March and July are relatively dry (<90 *mm* each). Rainfall over 1995 amounted to 3060 *mm* which was *c.* 25 % above the estimated long-term average of 2850 *mm* (J. R. Healey, *personal communication*; *National Meteorological Service of Jamaica* [1986]). The mean daytime (06:00–18:00 *h*) temperature was *c.* 17 °*C* with relatively little seasonal variation (*c.* 4 °*C*). Relative humidity varied comparatively little and was usually close to 85 %. The

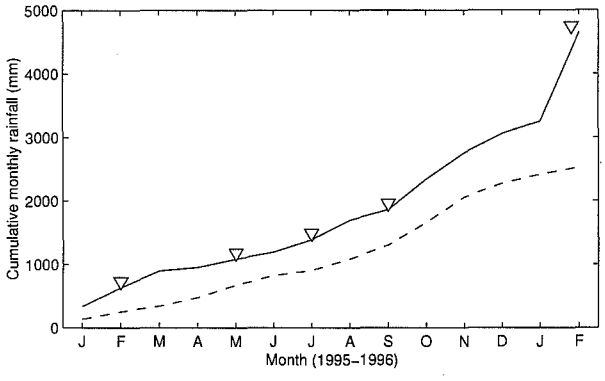

Figure 9.1: Cumulative monthly rainfall between January 1995 and February 1996 (solid line) in relation to the corresponding long-term averages (dashed line; J. R. Healey, *personal communication*) for Cinchona Botanical Gardens (at 1500 *m* a.s.l., *c.* 3 *km* SW of the forest plots). The downward triangles indicate the dates of litterbag collections.

climate of the study area has been described in detail in Chapter 4.

9.2.2 Litter decomposition experiment

Mature sunlit leaves from the dominant tree species *Cyrilla racemiflora*, *Lyonia* cf. *octandra*, and *Clethra occidentalis* were selected randomly from the canopy in both forests. Leaves that were severely damaged by herbivory, discoloured or having abnormal dimensions were not used. Litterbags (30×22 *cm*) were made from nylon gauze (5 and 1 *mm* mesh width for the top and bottom sections, respectively) and filled with 20 *g* (fresh-weight) each of *Cyrilla racemiflora* or *Lyonia* cf. *octandra* leaves whereas 15 *g* of fresh leaves were used per bag for *Clethra occidentalis*. The initial dry mass contained by each bag was computed using conversion factors based on oven-drying of eight fresh samples (15–20 *g*) per site and species.

On 21 December 1994, 27 litterbags per species per site were laid out randomly on the forest floor, distributed over three 5×5 *m* sub-plots per forest. Bags were retrieved after, successively, 49, 136, 200, 250, and 406 days of exposure (*cf.* Table 9.1). Per 27 bags, six replicates were retrieved in each of the first four collections and the remaining three at the end of the experiment, resulting in a total of 162 bags (6 or 3 replicates $\times$ 5 times $\times$ 3 species $\times$ 2 plots). After collection, the bags were weighed and a small sub-sample of known weight was taken for determination of dehydrogenase/microbial activity (see Section 9.2.4 for details). The remaining material was oven-dried (80 °*C* for 24 *h*) and the weight corrected for the removed sub-sample. The contents of the oven-dried litterbags were hand-sorted for roots and weighed again to the nearest 0.1 *g*. Mass loss was calculated as the difference between initial and final dry weights. Decomposition constants (k-values) were calculated using the single exponential

decay model of *Olson* [1963]:

$$W_t = W_0\, e^{-kt} \tag{9.1}$$

in which k denotes the decomposition constant (yr^{-1}), t the time (yr) and W_0 and W_t the mass at time 0 and time t, respectively. The initial and final litterbag masses were used to calculated k from Eq. 9.1.

In order to separate the influence of environmental differences between the two forests from those induced by the leaf material themselves, a cross-over experiment was carried out as well. The litterbags used in the cross-over experiment (72 in total, 6 replicates × 2 periods × 3 species × 2 plots) were recollected after 136 (6 May 1995) and 250 days (28 August 1995). The dried material was ground in a pulverisette (Fritsch, Type 05.202) and analyzed for total carbon and nitrogen using a Carlo Erba NA 1600 elemental analyzer.

9.2.3 Nitrogen nitrification and mineralization

Nitrification was determined using 14 PVC tubes of 20 *cm* length and 15 *cm* diameter per forest. The tubes were inserted *c.* 10 *cm* into the litter layer. After seven days, tilted perspex plates (30 × 30 *cm*) were installed 5 *cm* above the cylinders to avoid contamination by atmospheric deposition or additional litterfall while maintaining air exchange. Simultaneously, surface litter and topsoil material directly adjacent to the cylinders were sampled to establish the initial concentrations of NH_4-N, and NO_3-N. Final sampling was conducted after 16 and 13 days of incubation (from 8 to 24 January and from 7 to 20 February 1995). Samples were oven-dried (80 °*C* for 48 *h*) and homogenized. A 10 *g* sub-sample was extracted during 2 *h* of shaking in 100 *ml* of a 1.0 M KCl solution. After filtration (0.45 μm), samples for NH_4-analysis were acidified (0.7 *ml* HNO_3, 0.65 % Suprapure) to a final pH $\leq$2 [*Appelo and Postma*, 1993] and stored at 4 °*C* until analysis. Both NH_4-N and NO_3-N were determined colorimetrically (Skalar Auto Analyser). Net N-mineralization was calculated as final NH_4-N plus NO_3-N minus initial values and net nitrification as final NO_3-N minus initial NO_3-N [*Robertson and Vitousek*, 1981].

9.2.4 Soil biota and microbial activity

Fungal hyphae lengths and bacterial densities were determined on leaves of *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, and *Clethra occidentalis* contained in 3–4 litterbags per plot per species that had been placed on the forest floor for 136 days (from 21 December 1994 to 6 May 1995). Fungal lengths were measured after staining with 20 μl FITC/acetone/H_2O solution (5.0 *mg* : 1 *ml* : 199 *ml*) of a blended suspension of litter (0.5–2.0 *g*, fresh weight) in 60 *ml* McIlvaine-buffer kept at field pH. After filtration (45 μm), twenty random reticule fields ($n = 20$) were counted for fungal length under fluorescent light at 250 × magnification [*Faber et al.*, 1992]. Fungal length was approximated using a constant fungal radius of 1.65 μm [*Kjøller and Struwe*, 1982] whereas a density

factor of 0.33 $g\,cm^{-3}$ [*Van Veen and Paul*, 1979] and a carbon percentage of 45 % [*Swift et al.*, 1979] were used to estimate total carbon biomass.

Bacterial densities were counted in a litter/soil suspension (0.5–2.0 g, fresh weight) after staining with 4.0 mg DTAF in 20 ml $Na_2HPO_4.2H_2O$–NaCl buffer at pH = 9 of bacterial cell wall tissue on microscopic slides [*Hogervorst et al.*, 1997; *Berg*, 1997]. The actual counting was performed under fluorescent light after 1000 × magnification in twenty reticule fields per sample. For the conversion of number of bacteria to amounts of C stored in microbial biomass ($mg\,C\,g^{-1}$ dry weight of substrate), a constant factor of 0.64×10^{-11} mg C per bacteria was used [*Hunt and Fogel*, 1983].

Dehydrogenase activity (a commonly used measure of microbial activity; *Teuben and Roelofsma* [1990]) was determined on litterbag material that had been placed on the forest floor for 49 and 136 days by measuring formazan production in a 0.8 % triphenyltetrazolium chloride / Tris buffer (5.0 ml 0.1 M) / 1 g litter/soil solution (pH 7.6) [*Thalman*, 1968]. After incubation for 21 h at 30 $^{\circ}C$, the formazan was extracted with a 20 ml acetone/tetrachloride mixture (9:1 by volume). After filtration (45 μm), absorbance by triphenyl formazan (TPF) was measured spectrophotometrically at 480 nm relative to a formazan / soil solution series.

Soil respiration was determined by measuring the production of CO_2 and N_2O in PVC cylinders (n = 8 per forest; height 20 cm, diameter 15 cm) that were pressed into the litter layer for *c.* 10 cm. After seven days, the cylinders were closed with transparent covers containing a rubber septum. Gas samples were taken on 20 May and 12 June 1995 after 0, 1, 2, 4, 6, and 8 hours of incubation using a syringe. Samples were injected into standard glass tubes (venojects) filled with a known concentration of tracer gas and stored in the dark until transportation by air to the Department of General Microbiology, University of Copenhagen, Denmark, for gas chromatographical analysis. During the experiment soil temperature was measured every hour at 3 cm below the surface. After sampling had been completed, the head space within the cylinders (approximately 1800 cm^3) was measured and the contents of the cylinders collected in order to determine total dry-weight, water content (drying at 80 $^{\circ}C$, 24 h) and the organic fraction (as loss on ignition for sub-samples) of the contributing material. The initial concentrations and those after 8 h were used to determine rates of N_2O production. Because head space concentrations reached a maximum after 3–4 h only initial concentrations and those after 2 h were used to determine rates of CO_2 production. Daily rates were calculated by multiplying the average hourly rates times 24 h.

Soil mesofauna were extracted from 72 litterbags (6 replicates × 3 species × 2 forests × 2 periods) containing the same leaf species as used for the bacterial and fungal counts after exposure in the field for 200 and 250 days, respectively. Collections were made using open 'Tullgen-type' funnels [*Van Straalen and Rijninks*, 1982] and forced drying (during 5 days) under electric light bulbs. The collections were stored in a 70/5 mixture of alcohol and formaldehyde prior to identification at group level.

9.2.5 Statistical analysis

Litterbag data were analyzed in a three-way analysis of variance (*ANOVA*) to compare the effects of plot (PMull *vs.* MMor), species (*Lyonia* cf. *octandra vs. Cyrilla racemiflora, Clethra occidentalis*), and time (6 periods) on mass loss, total C concentrations, total N concentrations and dehydrogenase activity. The obtained k-values and microbial densities were subjected to two-way *ANOVA*s (plot, species). Tests for homogeneity and normal distribution were performed. Arcsin$\sqrt{x}$ transformations were used for all percentage data while data on density were log-transformed. Differences in nitrification, N-mineralization and contrasts in CO_2 and N_2O production were tested for significance (at the 95% probability level) using analyses of variance (*ANOVA*) and *t-test* statistics [*Sokal and Rohlf*, 1981] when sample sizes were small [*Spiegel*, 1972].

9.3 Results

9.3.1 Mass loss

The mean initial water contents of fresh leaves harvested in the PMull (61 ± 12 % of wet weight) and MMor forest (53 ± 4 %) was not significantly different. Mass loss, expressed as percentage of initial dry weight, for leaves from all three species, increased with time (Fig. 9.2). Contrasts in overall leaf decay rates per forest type differed significantly between species (*e.g. Lyonia* cf. *octandra vs. Cyrilla racemiflora* and *Clethra occidentalis* after 406 days in the MMor). The difference between *L. octandra* and the other two species was less pronounced in the PMull. Also, at the end of the experiment the total weight losses from *C. occidentalis* and *C. racemiflora* leaves in the MMor forest were 50 % lower than those found in the PMull ($P< 0.001$) whereas a relative reduction of *c.* 30 % was obtained for bags containing *L. octandra* leaves (Fig. 9.2). On average ($n = 3$ species) 56 % of the initial amount of PMull leaves was lost after 58 weeks of exposure in the PMull forest compared to a 32 % weight loss from the litterbags in the MMor. Because the interaction between plot×litter×time (Table 9.3) was significant as well ($P< 0.05$), no conclusions can be drawn from any of the two-way interactions.

The exponential decay constants k (yr^{-1}) were calculated at 0.66, 0.86, and 0.74 for, successively, *L. octandra*, *C. racemiflora*, and *C. occidentalis* leaves from the PMull forest, whereas k values of 0.44, 0.33, and 0.30 were derived for the corresponding materials from the MMor forest. On average ($n = 3$), k was 0.75 for PMull leaves *vs.* 0.35 for MMor material, suggesting that 53 and 30 % of the annually applied organic matter decomposes within a year in the respective forests.

Leaves of *L. octandra* and *C. racemiflora* collected in the PMull forest and left to decompose in the stunted MMor forest appeared to have lower rates of decomposition compared to non-exchanged litter that remained in the taller forest (Table 9.1). However, the contrasts were not significant (for *L. octandra* and *C. racemiflora*) or absent (for *C. occidentalis*). Contrasts in decomposition

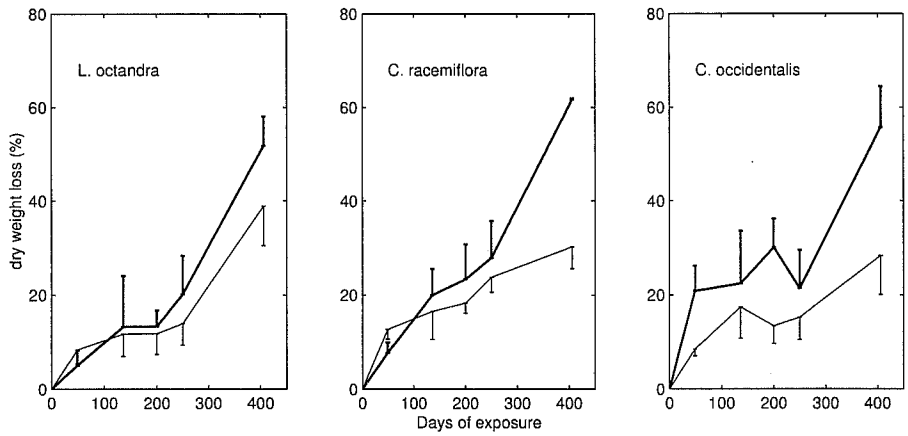

Figure 9.2: Temporal patterns of mean mass loss (percentage of initial dry weight; $n = 6$ except for the last series: $n = 3$) in litterbags containing mature leaves of *Lyonia* cf. *octandra*, *Cyrilla racemiflora* and *Clethra occidentalis* left to decompose for 49, 136, 200, 250, and 406 *days* (from 21 December 1994) in the PMull (bold line) and MMor forests (narrow line). Vertical lines represent one standard deviation.

rates between exchanged and non-exchanged leaves in the MMor were very small and, again, not significant (Table 9.3).

9.3.2 Carbon and nitrogen concentrations

Leaf material collected in the short-statured MMor forest showed a higher initial carbon content than that collected in the taller PMull (Table 9.2) and, in addition, a lower carbon loss during decomposition. The C content in MMor material decreased linearly by 2–3 % *vs.* 3–6 % in the PMull during the 58 weeks that the litterbags had been exposed in the field (Fig. 9.3). The interaction between plot×species (Table 9.3; $P < 0.001$) underlines the result that the C contents of the three species remained higher in the MMor forest than in the PMull throughout the year.

Nitrogen concentrations in fresh leaves of *L. octandra* and *C. racemiflora* were quite similar for the PMull and MMor forests but large contrasts were observed for N in leaves of *C. occidentalis* (2.16 % d.w. in the PMull *vs.* 0.95 % in the MMor). After 58 weeks, N content of the remaining material in the MMor litterbags had increased by 27–38 % (to 1.43, 1.20, 1.31 % dry weight for *Lyonia*, *Cyrilla* and *Clethra*, respectively) and by 51–55 % in the PMull for *Lyonia* and *Cyrilla* (to 1.63–1.43 % dry weight, respectively). However, litter from *C. occidentalis* collected in the PMull showed a surprising decrease of 23 %. Because the interaction plot×species×time was highly significant (Table 9.3), no conclusion can be drawn as to what were the main factors.

Table 9.1: Mean mass loss (percentage of initial dry weight) and standard deviations (in parentheses) in exchanged and non-exchanged litterbags containing mature sunlit leaves of *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, and *Clethra occidentalis* exposed for 136 and 250 days (from 21 December 1994) in the PMull and MMor forests.

Site of collection	Site of decomposition	Exposure (days)	Species *Lyonia*		*Cyrilla*		*Clethra*	
PMull	PMull	136	13.3	(10.7)	20.0	(5.6)	22.4	(11.2)
		250	20.1	(8.3)	27.9	(7.9)	21.4	(8.2)
PMull	MMor	136	8.6	(1.5)	15.3	(6.1)	22.8	(8.8)
		250	13.2	(1.4)	23.5	(4.8)	21.4	(6.4)
MMor	MMor	136	11.8	(4.8)	16.6	(6.0)	17.4	(6.6)
		250	13.9	(5.6)	23.8	(3.2)	15.3	(4.7)
MMor	PMull	136	12.1	(4.9)	16.8	(3.8)	12.6	(3.1)
		250	15.8	(8.0)	17.1	(7.6)	15.2	(6.3)

Table 9.2: The initial average nitrogen and carbon concentrations (% dry weight), C/N ratios and specific leaf areas (SLA, $cm^2\ g^{-1}$) of mature, sunlit *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, and *Clethra occidentalis* leaves from the PMull and MMor forests.

Site and species	Initial values C [%]	N [%]	C/N	SLA [$cm^2\ g^{-1}$]
PMull				
L. octandra	52	1.08	48	58±5
C. racemiflora	49	0.81	60	59±9
C. occidentalis	42	2.16	19	71±13
MMor				
L. octandra	51	1.00	51	62±8
C. racemiflora	50	0.71	70	63±11
C. occidentalis	48	0.95	51	74±9

Table 9.3: F-values for analyses of variance of dry weight loss (5 periods; $n = 159$, 3 bags missing), C and N concentrations (4 periods; $n = 122$, 4 bags missing) and dehydrogenase activity ($mg\,\mathrm{TPF}\,g^{-1}$ d.w.; 2 periods; $n = 72$) for plot (PMull and MMor), species (*L. octandra*, *C. racemiflora*, and *C. occidentalis*) and time. All values are significant at P< 0.001 unless indicated otherwise.

Variable	Plot	Species	Time	P×S	P×T	S×T	P×S×T
Weight loss(%)	45.7	13.0	70.6	7.5	6.7	2.5*	2.1*
C (% d.w.)	356.1	346.1	47.8	38.2	14.1	1.9^{ns}	0.9^{ns}
N (% d.w.)	938.2	502.8	37.2	503.1	5.2**	13.4	16.0
Dehydr. activity	8.4**	73.9	11.3**	5.3**	0.0^{ns}	6.3**	3.7*

*significant at P< 0.05; **significant P< 0.01; ^{ns}not significant.

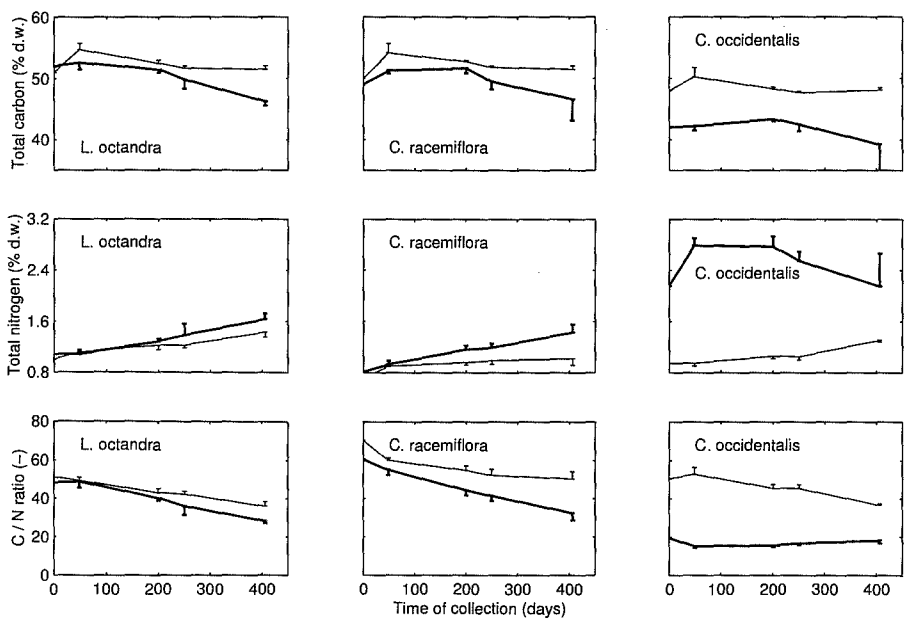

Figure 9.3: Average concentrations of total carbon and total nitrogen (% dry weight) in litterbag material (*Lyonia* cf. *octandra*, *Cyrilla racemiflora*, and *Clethra occidentalis*) after 49, 200, 250 ($n = 6$), and 406 *days* ($n = 3$) of field exposure in the PMull (bold lines) and MMor forests (narow lines). Vertical lines represent one standard deviation.

9.3.3 Nitrification and N-mineralization rates

The initial nitrogen concentrations and rates of transformation during two incubation experiments in each plot are listed in Table 9.4. Concentrations of NH_4-N were higher in the litter layer of the MMor forest whereas nitrate-N and both net-mineralization and net-nitrification were higher in the taller PMull forest ($P< 0.05$; *t-test*). Based on the changes in amounts of ammonium and nitrate after 16 and 13 *days* of incubation, no correlation between initial NH_4-N content and nitrification rate was observed. Production rates of NH_4-N and NO_3-N in the PMull litter layer were generally positive but those for the MMor forest were characterized by low nitrification and a very diverse ammonification (-25.3 to 26.8 $\mu g\, g^{-1} d^{-1}$). When the estimated daily rates of N-mineralization and nitrification are taken at face value and extrapolated to a one-year period, net N mineralization rates would amount to 2.92 and $-0.12\ mg\, g^{-1}\, yr^{-1}$ in the PMull and MMor, respectively; net ammonification to 2.77 and $-0.18\ mg\, g^{-1}\, yr^{-1}$, and net nitrification to 0.14 and 0.06 $mg\, g^{-1}\, yr^{-1}$. Using average bulk density values for the first 10 *cm* of the forest floor in the MMor and PMull forest of 0.07 and 0.22 $g\, cm^{-3}$ (*Kapos and Tanner* [1985]; Table 2.8), rates of net N-mineralization on an areal basis were estimated at 642 and $-8.4\ kg\, ha^{-1}\, yr^{-1}$ for the PMull and MMor, respectively; the corresponding net NH_4-N production at 610 and $-12.8\ kg\, ha^{-1}\, yr^{-1}$, and the net production of NO_3-N at 30.5 and 4.3 $kg\, ha^{-1}\, yr^{-1}$.

9.3.4 Soil biotic densities and activity

Table 9.5 summarizes the observations of bacterial density and fungal hyphae length in litterbags containing leaves of *L. octandra*, *C. racemiflora* or *C. occidentalis* that had been exposed in the field for 136 *days*. Bacterial densities in the litterbags retrieved from the PMull forest were 2–8 times higher than in those from the MMor forest ($P< 0.05$, *t-test*). However, bacterial densities in natural litter samples taken from the two forests were virtually identical (Table 2.6). Although bacterial densities were determined for litter that had been exposed for 136 days only (second date of collection in Fig. 9.2) they corresponded with observed patterns of decomposition in that most bacteria were found in the relatively rapidly decomposing and nitrogen-rich substrate derived from *C. occidentalis*. This pattern remained intact when the substrate was exchanged (Table 9.5).

Fungal lengths in *C. racemiflora*, *L. octandra* and *C. occidentalis* material were not significantly different between the two forests (fungal length in *Clethra* litter in the PMull was more than twice the value observed for the MMor but standard errors were >50 %). A highly significant and positive correlation was found between log-transformed fungal length and pH of the substrate ($r^2 = 0.20$, $P< 0.001$, $n = 52$, all species, plots and exchanged litter included). The correlation remained significant for both exchanged and non-exchanged MMor material ($r^2 = 0.33$ for non-exchanged and $r^2 = 0.41$ for exchanged litter, $P< 0.05$, $n = 15$) but was absent for PMull material. Neither was there a

Table 9.4: Averages values and ranges (in parentheses; n = 10–14 useful measurements per period) of initial inorganic nitrogen concentrations ($\mu g\, g^{-1}$) and rates of transformation ($\mu g\, g^{-1} d^{-1}$) in 10 cm deep litter and topsoil columns. Incubations were performed between 8 and 24 January 1995 and 7 and 20 February 1995.

Site	Period	Initial concentration		Final concentration		Net NH_4-N production	Net NO_3-N production	Net N mineralization
		NH_4-N	NO_3-N	NH_4-N	NO_3-N			
		$\mu g\, g^{-1}$		$\mu g\, g^{-1}$			$\mu g\, g^{-1} d^{-1}$	
PMull	8–24/1	197[a] (85-445)	8.1 (3.2-18.7)	324[e] (147-464)	15.3[g] (3.9-27.3)	7.9 (-9.0, 21.5)	0.46[k] (-0.09,1.11)	8.4 (-8.2, 20.9)
	7–20/2	267 (123-403)	12.9[c] (3.0-32.7)	361 (147-502)	17.1[f] (2.7-43.9)	7.3[i] (-6.8, 20.4)	0.32 (-0.51, 1.36)	7.6[m] (-6.0, 20.4)
	Average	235[b]	10.6[d]	343	16.2[h]	7.6[j]	0.38[l]	8.0[n]
MMor	8–24/1	545[a] (300-823)	6.0 (3.6-10.6)	698[e] (448-996)	7.2[g] (5.2-10.3[i])	9.0 (-11.3, 26.8)	0.08[k] (-0.25, 0.25)	9.1 (-12, 27)
	7–20/2	384 (187-696)	6.6[c] (2.5-15.3)	228 (77-472)	10.3[f] (4.2-23.0)	-11.9[i] (-25.3, -0.8)	0.29 (-0.57,1.49)	-11.6[m] (-25.6, 0.7)
	Average	471[b]	6.2[d]	480	8.6[h]	-0.5[j]	0.17[l]	-0.33[n]

[a,b..n] values carrying the same superscript letter are significantly different between forests.

Table 9.5: Average bacterial densities and fungal hyphae lengths (and their standard deviations) and pH of substrate in non-exchanged and exchanged litterbags (n = 3–4 per species per plot) containing leaves of *Lyonia* cf. *octandra*, *Cyrilla racemiflora* and *Clethra occidentalis* after 136 *days* of field exposure. Density values are expressed in numbers (bacteria) or meters (fungi) per gram dry weight of substrate.

Site of collection	Site of decomp.	Species	Bacteria		Fungi		pH ranges
			numbers $10^9\,g^{-1}$	biomass $\mu g\,C\,g^{-1}$	length $m\,g^{-1}$	biomass $mg\,C\,g^{-1}$	-
PMull	PMull	*Lyonia*	0.68±0.14	44±9	525±156	0.67±0.20	6.1–6.1
		Cyrilla	0.98±0.42	62±27	1189±641	1.51±0.81	5.3–6.0
		Clethra	5.30±2.33	339±149	707±484	0.90±0.62	6.8–7.2
PMull	MMor	*Lyonia*	0.41±0.26	26±17	312±125	0.40±0.16	5.9–6.2
		Cyrilla	0.69±0.38	44±24	1034±566	1.31±0.72	5.3–6.1
		Clethra	3.84±1.56	256±100	327±155	0.42±0.20	6.7–7.4
MMor	MMor	*Lyonia*	0.35±0.33	22±21	424±133	0.54±0.17	5.7–6.8
		Cyrilla	0.33±0.20	21±13	1087±361	1.38±0.46	5.3–5.5
		Clethra	0.67±0.32	43±21	324±173	0.41±0.22	6.5–7.2
MMor	PMull	*Lyonia*	0.17±0.02	11±1	514±244	0.65±0.31	6.0–6.7
		Cyrilla	0.24±0.08	15±5	950±365	1.21±0.46	5.4–5.6
		Clethra	0.38±0.02	24±1	245±119	0.31±0.15	6.5–7.1

significant relationship between pH and bacterial numbers. Surprisingly, for all plots and species the exchanged substrate gave lower bacterial and fungal densities than material that was left in the site of origin even though pH values were not affected (Table 9.5). However, none of the differences were significant.

Biotic biomass was heavily dominated by fungi (Table 9.5). Fungal biomass in non-exchanged substrates ranged from 0.41 $mg\,C\,g^{-1}$ in *C. occidentalis* in the MMor to >1.5 $mg\,C\,g^{-1}$ in *C. racemiflora* in the PMull. Bacterial biomass in non-exchanged litter generally ranged between 21–62 $\mu g\,C\,g^{-1}$ but was exceptionally high for *C. occidentalis* in the taller forest (339 $\mu g\,C\,g^{-1}$). The biotic total biomass of 0.56–0.71 $mg\,C\,g^{-1}$ in *L. octandra* and 1.40–1.57 $\mu g\,C\,g^{-1}$in *C. racemiflora* material, did not differ dramatically between the two plots. For *Clethra occidentalis*, however, the contrast was large (0.46 $mg\,C\,g^{-1}$ in the MMor *vs.* 1.24 $mg\,C\,g^{-1}$in the PMull; Table 9.5).

Dehydrogenase activity (Fig. 9.4) showed significant differences between species (P< 0.001) but generally did not reveal significant contrasts between forest plots or length of litterbag exposure (*i.e.* 49 or 136 *days* as sampled on 8 February and 8 May 1995, respectively). However, dehydrogenase activity in litterbags that contained *Clethra occidentalis* leaves from the MMor forest was nearly twice as high in PMull material. A similar contrast was found for *C. occidentalis* material sampled in February 1995 (after 49 *days* of exposure) compared to May (after 136 *days* of exposure). The PMull/MMor contrast, however, was again not significant. Exchange of litter did not significantly affect dehydrogenase activity in most cases either. However, average activity in

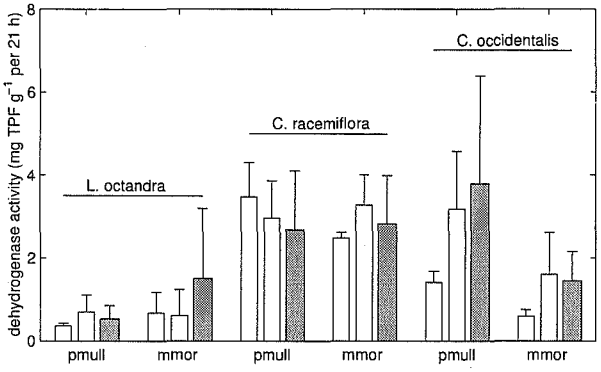

Figure 9.4: Average dehydrogenase activity and standard deviations (n = 4–6) for (a) litter of three species left to decompose for 49 and 136 days in the site of origin (first and second light bars) and (b) exchanged litter that was incubated for 136 days in the contrasting location (dark bars). Dehydrogenase activity expressed as formed triphenyl formazan (TPF) after incubation for 21 h.

L. octandra litter from the PMull forest appeared to be higher when left to decompose in the MMor forest rather than in the PMull itself (Fig. 9.4). For the complete second harvest (including all species, plots and cross-experiment litter) mass loss and dehydrogenase activity were well correlated (r^2 = 0.20, P< 0.01, n = 42). Correlation, however, was absent when only PMull substrate was considered (crossed litter excluded) but reasonable for MMor material (r^2 = 0.25, P< 0.05, n = 23).

Table 9.6 summarizes the results of measurements of CO_2 production in the litter layers of the PMull and MMor forests. Although the standard errors are large and the difference is not statistically significant, respiration in the PMull forest appears to be higher than in the MMor. On average (n = 5 dates) soil respiration was estimated at 79±10 and 46 ±15 in the PMull and MMor forest, respectively (equivalent to 1.90 and 1.10 $g\,CO_2\,m^{-2}\,d^{-1}$). Extrapolation of these average values to obtain approximate annual estimates gave 694 and 402 g CO_2 production $m^{-2}\,yr^{-1}$. Average moisture content of PMull litter was *c.* 20 % higher than in the MMor. As could be expected, differences in soil temperature between the two plots were minimal but amounts of organic matter that contributed to soil respiration showed large differences. The top 10 cm of the PMull soil and litter column had a mean loss on ignition of 51±19 % d.w. (n = 8 cylinders) *vs.* 95±5 % in the MMor (Table 9.6). This difference reflects the different depth of the ectorganic horizons in the two plots. About 40% of the column in the PMull consisted of mineral soil whereas in the MMor the cylinders contained organic material only. Four sample sets were analyzed for the production of N_2O. On average, the production of N_2O amounted to 59 and 17 $\mu g\,m^{-2}d^{-1}$ in the PMull and MMor, respectively, or 21.5 and 6.2 $mg\,m^{-2}\,yr^{-1}$ when extrapolated to annual production rates. These denitrification losses represent less than 0.5 and 0.9 % of the annually produced NO_3-N

Table 9.6: Soil respiration (CO_2 production, $g\,m^{-2}\,d^{-1}$; N_2O production, $\mu g\,m^{-2}\,h^{-1}$), mean litter temperature ($^{\circ}C$), moisture- (%) and organic matter content (represented by loss on ignition LOI, %). Values are means ($n = 8$) with standard deviations in parentheses.

Site	Date	CO_2	N_2O	Temp.	Soil moisture	LOI
		$mg\,m^{-2}\,h^{-1}$	$\mu g\,m^{-2}\,h^{-1}$	$^{\circ}C$	% w.w.	% d.w.
PMull	25/01/95	73 (32)	2.7	14.0	77	-
	17/02 ,,	81 (27)	4.5	13.6	72	-
	20/05 ,,	76 (28)	1.2	-	62	47.3
	12/06 ,,	68 (11)	1.3	-	51	53.9
	06/09 ,,	98 (33)	-	16.3	86	-
	Average	79 (10)	2.5	14.6	70	50.6
MMor	25/01/95	47 (19)	0.04	13.5	56	-
	17/02 ,,	45 (14)	0.71	13.7	50	-
	20/05 ,,	51 (14)	1.0	-	54	93.6
	12/06 ,,	21 (14)	1.0	-	53	96.6
	06/09 ,,	66 (38)	-	16.7	79	-
	Average	46 (15)	0.71	14.6	58	95.1

in the PMull and MMor forests, respectively, and are not considered further, therefore.

Table 9.7 gives an overview of the species richness and mean density values of 30 principal taxonomic groups of soil mesofauna as observed in the litterbags containing leaves of *Lyonia*, *Cyrilla*, and *Clethra* in the PMull and MMor forests. Fungivores (such as *Cryptostigmata* and Collembola) and predating Coleoptera were most abundant in litterbags in the PMull forest. *Staphylinidae* were found to make up 80 % of the beetles present in the PMull forest *vs.* only 33 % in the MMor. Inter-site differences were large for saprovores, especially for comminutor groups like Diplopoda and Isopoda; moderate for herbivores and small for the carnivorous faunal groups (Araneae, Pseudoscorpionida, Formicidae and Coleoptera larvae), except for centipedes (Chilopoda, absent in MMor substrates). For Isopoda, Diplopoda, and Diptera larvae the highest densities were found in the PMull. Formicidae (ants) were found only in very small numbers, Isoptera (termites) were distinctly absent from the litterbags. Nematoda (roundworms) and Enchytraeidea (potworms) were relatively abundant but were not included in the identifications.

9.4 Discussion

9.4.1 Leaf-litter decomposition

Because of the often excessive rainfall, leaching from litterbags placed on the forest floor in tropical rain forests may be high, and this often leads to unrealistically high mass losses [*Olson*, 1963; *Swift et al.*, 1979; *Gunadi*, 1993]. The derived turn-over coefficients may exceed a value of 1.0, suggesting that over 63 % of the litter decomposes in one year or less. In montane forests decomposition

Table 9.7: Species richness and population density for 30 principal soil fauna groups in litterbags containing foliar material of *Lyonia* cf. *octandra*, *Cyrilla racemiflora*, or *Clethra occidentalis* in PMull and MMor forest. Litterbags (6 per species) were removed after 200 and 250 days of field exposure. Density values (number of individuals) represent 36 (6 replicates×3 species×2 periods) bag averages, standardized to no. per m^2 per 100 g residual substrate. The numbers of observed species represent totals over 36 bags. Nematoda (roundworms) and Enchytraeidea (potworms) were not included in the identifications.

Class and Order	Sub-order	PMull		MMor	
		Species	Density	Species	Density
		no.		*no.*	
Annelida (segmented worms)					
Oligochaeta (earthworms only)		3	1	1	<1
Gastropoda (slugs & snails)		1	15	1	6
Crustacea					
Isopoda (woodlice)		4	18	4	2
Amphipoda (sandhoppers)		2	19	2	5
Myriapoda					
Chilopoda (centipedes)		2	4	-	-
Diplopoda (millipedes)		3	24	2	9
Arachnida					
Acari (mites)	Cryptostigmata	56	1374	49	928
	Pro/Mesostigmata	52	1031	46	1202
	Ixodidae	1	1	1	4
Araneae (spiders)		19	19	13	22
Opiliones (harvestmen)		-	-	1	1
Pseudoscorpionida		1	<1	-	-
Insecta					
Thysanura (silverfish)		1	<1	1	2
Coleoptera (beetles)		32	343	25	209
larvae		15	16	11	18
Collembola (springtails)		67	2041	49	898
Orthoptera (grasshoppers, crickets)		2	5	3	2
Dictyoptera (cockroaches)		1	9	1	6
Diptera (flies & midges)	Brachycera	6	11	7	7
	Larvae	10	41	6	9
	Nematocera	20	180	19	85
	Larvae	6	42	4	6
Heteroptera (bugs)		9	44	5	5
Homoptera (cicadas)		8	31	6	21
Hymenoptera	Formicidae (ants)	1	<1	1	1
	Others (bees, wasps)	17	202	16	143
Lepidoptera (butterflies, moths)		5	9	7	7
Larvae		5	27	6	15
Psocoptera (booklice)		1	7	1	7
Thysanoptera (thrips)		3	11	2	16
Various		8	13	7	13
Totals		361	5548	297	3649

is usually slower compared to lowland areas and this has been attributed to, *inter alia*, lower temperatures, persistent wetness (the absence of wetting-drying cycles) and poor substrate quality (including low concentrations of nitrogen and high concentrations of phenolic compounds), [*Grubb*, 1977; *Tanner*, 1981;

Edwards, 1982; *Vitousek*, 1984; *Bruijnzeel et al.*, 1993].

The decay rates obtained in the present study using litterbags have their limitations. The least satisfactory aspect of the decomposition experiment is the use of mature, sun-lit leaves as initial substrate. Mature leaves from the top of the canopy tend to have a different leaf mass per unit area and nutrient composition than leaves further lower down in the canopy [*Roberts et al.*, 1999]. Also, the use of fresh leaves bypasses retranslocation effects on nutrient and carbon concentrations that would be included if freshly fallen litter had been used (which, in addition, would have originated in the upper and lower canopy alike). Live leaves therefore represent a different starting point for decomposition than actual freshly fallen litter. As demonstrated in Table 3.2, concentrations of Ca and Al (but not Mg) generally increase with leaf age in the study area whereas concentrations decrease for N (by 10–15 %), K (by 70 %) and P (by 40 %). Based on nutrient analysis of leaf and fresh litter material collected in April 1997 for seven principal tree species, including the three used in the litterbag experiment, retranslocation of nutrients appeared to be moderate for *Lyonia* cf. *octandra*, nearly absent for *Cyrilla racemiflora* and high for *Clethra occidentalis* (*cf.* Section 8.4.5). Nevertheless, mature foliage was preferred over litter material in order to (i) improve the homogeneity (age) and identity of the initial substrate, (ii) obtain sufficient material at once and (iii) avoid conservation procedures (*e.g.* drying) that would have interfered with the decomposition process [*cf. Tanner*, 1981].

Litterbags may affect decomposition rates by altering the micro-climate around the decaying substrate, by hindering substrate/soil contact, and by the exclusion of some soil (macro) fauna [*Swift et al.*, 1979; *Cornejo et al.*, 1994]. Generally, the contents of litterbags will show slower decomposition rates compared to substrates left to decompose in the open [*Coleman and Crossley*, 1996] but in this study such effects are believed to be small. For example, working in the same area *Tanner* [1981] demonstrated that litter enclosed in bags remained wetter compared to leaves outside. Whilst less variable moisture contents may induce more favourable conditions for microbial activity and therefore higher decomposition rates [*Vossbrinck et al.*, 1979] no such effect emerged [*Tanner*, 1981]. Also, the large mesh width of the top side (5 *mm*) of the presently used bags effectively allowed access as most mesofauna groups appeared to be present in reasonable numbers (Table 9.7). However, exclusion of such macro-fauna like Araneae (spiders), Chilopoda (centipedes), Dictyoptera (cockroaches), Oligochaeta (*e.g.* earthworms) and Orthoptera (grasshoppers and crickets) cannot be ruled out completely (*cf.* Table 9.7).

Decomposition of organic material in the litterbags occurred at a faster rate in the moderately tall-statured PMull forest than in the stunted MMor forest (Fig. 9.2). Also, two out of three species (*Lyonia* cf. *octandra* and *Cyrilla racemiflora*) tended to decompose at a slower rate when material was transferred from the PMull forest to the MMor forest but the opposite effect was not found when leaves from the MMor were transferred to the PMull (Table 9.1). No exchange effects were found for *Clethra occidentalis* leaves. Thus, the slower decay of leaves in the MMor forest seems to be influenced by both species char-

acteristics and plot conditions. However, the significant differences in mass loss for the three species were not clearly related to differences in initial N concentrations, C/N ratio or specific leaf area (SLA). Decomposition rates of *Cyrilla racemiflora* leaves were relatively high considering the low initial N and high C/N ratios (Table 9.2). By contrast, leaves of *Clethra occidentalis* had high N, a low C/N ratio and a relatively high SLA but did not show noticeably higher rates of decomposition in either forest (Fig. 9.2). Initial N concentrations of *C. occidentalis* were remarkably high in the PMull forest and remained high despite a decrease in concentration during the second half of the experiment (Fig. 9.3). Unlike concentrations of K and P, which usually decrease early in the decomposition phase [*Swift et al.*, 1979; *Anderson et al.*, 1983], concentrations of N in decomposing *L. octandra* and *C. racemiflora* leaves (as well as in *C. occidentalis* leaves in the MMor forest) increased steadily during exposure in the field (Fig. 9.3) which is in agreement with earlier reports that N is immobilized and accumulated by microorganisms during decomposition [*Berg and Staaf*, 1981; *Anderson et al.*, 1983; *Cuevas and Medina*, 1988]. In this respect, the persistent decrease in N concentrations in decomposing *C. occidentalis* leaves in the PMull forest is all the more surprising given the high bacterial densities observed in this particular substrate (Table 9.5). However, this could point to a transition from immobilization of N to N-mineralization which occurs at higher N levels [*Berg and Staaf*, 1981]. In view of the fact that the high N concentrations in *C. occidentalis* substrate in the PMull were consistent for all litterbags, it is difficult to believe that these would be the result of some sort of contamination. Also, the fact that not only N concentrations but also concentrations of polyphenols were highest in fresh *Clethra* leaves (Table 3.13) does not support the hypothesis of *Bruijnzeel et al.* [1993] that reduced N supply in montane forests stimulates the production of polyphenols in foliage that tend to retard decomposition, although lower concentrations of N in leaf fall in the MMor were indeed accompanied by higher concentrations of phenols (Table 8.4).

The average decomposition rates obtained with the litterbag approach (53 % and 30 % disappearance per year for the PMull and MMor, respectively) are well below previous estimates for the two forests based on the ratio between annual leaf litterfall and leaf-litter standing crop (136–90 %, respectively; Section 8.4.2). *Tanner* [1981] obtained litterbag-based rates of 36 % for his stunted Mor forest and 42 % for tall-statured Mull forest during the first year of decomposition. Although these values are similar to the presently obtained estimates, their relative ranking (PMull$\gg$Mull>Mor>MMor) does not entirely match the ranking according to forest stature.

For almost all species, *Tanner* [1981] found decomposition to be more rapid in the nutrient-rich Mull Ridge forest. Also, Mor material that was left to decompose in the Mull Ridge forest decomposed at faster rates than material that was not transferred whereas Mull litter decomposed at slower rates when transferred to the Mor Ridge forest. Our litterbag cross-over experiment produced less consistent results (Table 9.1). This can be explained partly by the limited time that exchanged substrates were exposed in the field in the present study. Inter-site contrasts for non-exchanged litter became significant after 406 days

only (Fig. 9.2). At 383 days, the duration of the cross-over experiment by *Tanner* [1981] was probably sufficient to expose potential differences whereas the 136 and 250 day periods used in the present study were not. Also, given the intermediate character of the PMull and the MMor forests (in many respects) in the overall sequence of forest types in the study area (Chapter 2), the contrasts between the two can be expected to be less pronounced than those between the 'end members' of the sequence studied by *Tanner* [1981].

9.4.2 Soil microbial abundance and activity

Like the results of the litterbag cross-over experiment, our data on soil biotic biomass and activity must be treated with caution as they were obtained at a time when differences between plots had not yet fully developed (*cf.* Figs. 9.1 and 9.2). Microbial activity depends primarily on the moisture status and quality of the substrate [*Cornejo et al.*, 1994]. Although differences in bacterial densities associated with the different species did not reflect the differences in corresponding decay constants, the number of bacteria were invariably smaller in the MMor forest in each case (Table 9.5). Densities of bacteria (and fungi) seem to be dictated by litter quality, as exchanged leaves from both the PMull and the MMor plots did not experience significantly altered colonisation compared to leaves that decomposed at the site of origin (Table 9.5). Also, the highest numbers of bacteria were observed in decaying leaves of *Clethra occidentalis* which also had the highest concentrations of N (Tables 9.2 and 9.5). C/N ratios have been widely used as an index of resource quality for the microbial community (*Berg* [1997] and references therein). Because population densities decreased with any given exchange of substrate (Table 9.5), the soil biota of the study area seems to be adapted to the specific physical and chemical characteristics of the litter present in the PMull and MMor forests.

The high fungal density found on decaying leaves of *Cyrilla racemiflora* is probably responsible for the relatively high mass loss (after 136 days) found for this species. In fact, loss rates were comparable to those for the much more N-rich *Clethra* leaves (Table 9.1). Decaying leaves of *C. racemiflora* had a relatively high C/N ratio (Table 9.2) but a low pH compared to the other species. The high values for fungal lengths in *Cyrilla* leaf litter agree with other observations of increased fungal biomass on increasingly acidic substrates in tropical forests [*e.g. Cheng Yang and Insam*, 1991]. Similarly, the higher bacterial densities (and lower acidity; Table 9.5) of *Clethra* litter confirm the general idea that bacterial activity decreases with increasing acidity [*Sylvia et al.*, 1998].

It is generally accepted that bacteria play a dominant role as primary decomposers in mull-type soils, while fungal activity is thought to be dominant in Mor-type soils [*Tamm*, 1991]. Although fungal lengths in the litterbags in the PMull forest were slightly higher than in the MMor forest (also in the cross-over experiment), they were much higher (by a factor 4.3) in natural litter in the MMor forest (compare Tables 2.6 and 9.5) thus conforming to previous studies [*Tamm*, 1991]. However, the relative dominance of fungi may to some extent be a seasonal effect as the microbial density counts were performed dur-

ing relatively dry conditions (Fig. 9.1). Drought is known to stimulate fungal activity [*Edwards*, 1977; *Cornejo et al.*, 1994] but further work would be needed to evaluate such effects in the present case. At 0.5–1.6 $mg\,C\,g^{-1}$ the average amounts of total bacterial and fungal biomass in non-exchanged litter material are higher than the 0.25–0.7 $mg\,C\,g^{-1}$ usually found in tropical topsoils [*Cheng Yang and Insam*, 1991]. This is mainly due to the fact that the present values pertain to the litter layer rather than the soil. Because faunal biomass tends to decrease with depth [*Hunt et al.*, 1987; *Berg*, 1997], an overestimation compared to topsoil values is expected.

Dehydrogenase activity for the various types of leaf litter correlated reasonably well with mass losses and microbial density, *i.e.* low values for *L. octandra*, high values for *C. racemiflora* and intermediate values (with considerable contrasts between the PMull and MMor) for *C. occidentalis* (Fig. 9.4). Interestingly, only the latter species tends to show contrasts between material from the MMor and PMull that were also found for density of bacteria and fungi (Table 9.5). The good correlation between mass loss and dehydrogenase activity (Section 9.3.4) is consistent with the reputation of the latter as a useful proxy for decomposition and microbial activity [*Teuben and Roelofsma*, 1990].

Carbon dioxide emission by soil micro-biota, fauna, and roots (soil CO_2 efflux or soil respiration [*Anderson et al.*, 1983]) has been proposed as an indirect measure of net primary productivity of a forest [*Warner*, 1970]. The estimated annual CO_2 production in the PMull and MMor forests (694 and 402 $g\,CO_2\,m^{-2}\,yr^{-1}$) are comparable to the rates reported for temperate deciduous forest and dry tropical forest (600–800 $g\,CO_2\,m^{-2}\,yr^{-1}$) but are at the low end of the spectrum (500–5000 $g\,CO_2\,m^{-2}\,yr^{-1}$) for moist tropical forests, including montane cloud forest [*Raich and Schlesinger*, 1992; *Cavelier and Peñuela*, 1990; *Singh and Gupta*, 1977, *cf.* Table 9.8]. The presently derived rates are also high compared to the production of CO_2 associated with the disappearance of litter. Given an annual leaf litter input of 5.12 $t\,ha^{-1}$ in the PMull forest (Table 8.1), together with an annual decay rate of 53 % (litterbag estimate, Section 9.3.1) and an initial carbon content of *c.* 48 % (Table 9.2), an annual production of about 480 $g\,CO_2\,m^{-2}\,yr^{-1}$ is estimated. This would suggest that *c.* 70 % of the total measured respiration of 694 $g\,CO_2\,m^{-2}\,yr^{-1}$ would be derived from litter decomposition. The remaining 30 % of the soil respiration must be derived from respiration from roots and their symbionts, from respiration from microbes decomposing root exudates and dead roots, and from soil fauna [*Schlesinger*, 1977; *Singh and Gupta*, 1977; *Kursar*, 1989; *Cavelier and Peñuela*, 1990]. Repeating the exercise for the MMor forest (4.62 $t\,ha^{-1}$ leaf litterfall, 30 % decomposition per year, 50 % C), suggests a CO_2 production of 254 $g\,m^{-2}yr^{-1}$, *i.e.* 64 % of the estimate derived from direct measurements.

Both calculations neglect any contributions from decomposing wood and trash fall but considering the dominance of leaf fall (>75 % of total litter fall; Table 8.1) and the contrasting decay rates of the respective litter fractions, the underestimation is believed to be small. Studies in tropical and temperate forests suggest that 30–70 % of the total soil respiration may be derived from carbon translocated to the roots [*Schlesinger*, 1977; *Singh and Gupta*, 1977;

Table 9.8: Mean rates of soil respiration in different types of tropical forest

Location	Forest type	Respiration rates $mg\,CO_2\,m^{-2}\,h^{-1}$
Lake Aecham, Australia[1]	LRF	570
Barro Colorado, Panama[2]	LRF	460–680
Bako, Sarawak[3]	LRF	223
Gunung Mulu, Sarawak[4]	LRF	242
	Heath forest	307
Serrania de Macuira, Colombia[5]	Dry forest	251
	Cloud forest	511
Tjibodas, Indonesia[6]	LMRF	169
PMull, Jamaica[7]	UMRF	79
MMor, Jamaica[7]	UMRF	46

LRF lowland rain forest; LMRF lower montane rain forest; UMRF upper montane rain forest. [1]*Maggs and Hewett* [1990]; [2]*Kursar* [1989]; [3]*Warner* [1970]; [4]*Anderson et al.* [1983]; [5]*Cavelier and Peñuela* [1990]; [6]*Warner* [1970]; [7]present study.

Kursar, 1989] whereas *Maggs and Hewett* [1990] reported that the contribution of root respiration to total forest floor respiration was generally 75–85 %. As such, the presently derived litter respiration contributions of 70 % (PMull) and 63 % (MMor) may represent an underestimation of total forest floor respiration rates derived for both forests. In the MMor, the measuring cylinders only contained litter (and perhaps part of the fragmentation layer) whereas the cylinders installed in the PMull forest contained approximately 40 % (by volume) mineral topsoil material as well. As with decomposition, soil respiration tends to be determined by the quality and quality of the contributing substrate. Similar situations in which habitat differences instead of climatic conditions caused different CO_2 respiration rates have also been reported for other locations [*Schlesinger*, 1977; *Singh and Gupta*, 1977]. The differences were attributed to contrasts in edaphic conditions, plant density, and physical/chemical quality of the litter substrate [*Rout and Gupta*, 1989].

9.4.3 Soil fauna

Higher diversity, but also abundance of soil faunal groups in litterbags generally coincide with higher decomposition rates [*Wallwork*, 1970; *Berg*, 1997]. In the present study, the dominance of fungi in biotic biomass in the litterbags (highest in the PMull) was paralleled by the occurrence of fungivores and their predators (Table 9.7). Not surprisingly, both Collembola (springtails) and Acari (mites) were the most abundant (meso)-faunal groups in both forests, which may directly affect the numbers of predators (mainly *Staphylinidae*) among the Coleoptera (beetles) and Chilopoda (centipedes). The contrasting densities of fragmenters such as Isopoda (woodlice), Diplopoda (millipedes), and Diptera larvae (flies and midges) which were all higher in the PMull, are likely to be responsible for the more rapid decay of litter in the taller forest (Table 9.7, Fig. 9.2). Given the relatively large size of millipedes compared to

other groups, the inter-site contrast would increase significantly if the number of fragmenters would be expressed in terms of biomass per unit area/weight of substance instead of frequency of occurrence only. The distinct absence of *Isoptera* (termites) and the low values for *Formicidae* (ants) in the study forest are typical for the majority of tropical montane forest ecosystems [*Janzen*, 1983; *Olson*, 1994]. Hymenoptera (other than ants, *e.g.* wasps) and adult Diptera were present in considerable numbers in both forests, despite escape possibilities from the litterbags during the extraction procedure. Apparently, winged adults experience ground dwelling conditions favourable enough for their reproduction. Oligochaeta (*e.g.* earthworms), which are important for decomposition and redistribution of organic matter [*Lee*, 1985; *Hendrix*, 1995] as well as soil aeration under wet conditions [*Gill*, 1969; *Cavelier and Peñuela*, 1990] were only found in too small numbers to allow a useful interpretation.

9.4.4 Nitrogen mineralization and nitrate production

The presently found concentrations of NH_4-N in the top 10 *cm* of the soil (including ectorganic layers; Table 9.4) are only half those reported by *Tanner* [1977b] for the nearby Mor- and Mull Ridge forests, whereas concentrations of NO_3-N in the stunted Mor Ridge forest were also higher, again in contrast with the present findings (Table 9.9). However, both studies are consistent with the contention of *Richards et al.* [1985] that NH_4-N is dominant over NO_3-N in mor -type soils. Compared to studies conducted in (sub)montane forests in Costa Rica [*Marrs et al.*, 1988], Hawaii [*Vitousek et al.*, 1983], and Malaysia [*Chandler*, 1985], the present initial amounts of NH_4-N and NO_3-N are about 6–100 times higher (Table 9.9). *Tanner* [1977a] explained the high levels of mineral N in the Jamaican forest soils by their relatively high cation exchange capacity (CEC) and thus NH_4^+-binding ability. Indeed, the CECs reported by *Tanner* [1977a] (120 and 185 $m\,eqper 100\,g$ for Mull- and Mor Ridge forest, respectively) rank highest among the wide range of tropical montane forest soils discussed by *Bruijnzeel and Proctor* [1995] but the CECs of the present ectorganic layers (27 to 59 $m\,eq.100\,g^{-1}$; Table 2.10 in Chapter 2) only assume an intermediate ranking.

Because the inorganic pools of N present in a soil may turn over quite rapidly, the rate of nitrogen mineralization, *i.e.* the N-supplying potential of the soil, is often considered a better indicator of N-availability [*Keeney*, 1980; *Powers*, 1980]. Nitrate production rates in the PMull were about twice those in the MMor but rates of net N-mineralization in the two forests were very different (Table 9.4). The present rates of net mineralization for the PMull were twice those found by *Tanner* [1977a] for the Mull Ridge forests and much higher than the rates obtained by *McDonald* [2000] for secondary lower montane forest in the area. The present nitrification rates were almost 10 times lower than those previously obtained by *Tanner* [1977a] in the corresponding forest types but of the same order of magnitude as reported for other montane forests [*McDonald*, 2000; *Marrs et al.*, 1988; *Vitousek et al.*, 1983, *cf.* Table 9.9]. The high nitrification rates derived by *Tanner* [1977a] are most likely related to the fact that

Table 9.9: Concentrations of mineral nitrogen (NO_3-N and NH_4-N, $\mu g\, g^{-1}$) and total nitrogen (%) in topsoil material plus net rates of mineralization and nitrification ($\mu\, g\, g^{-1} 14\, d^{-1}$) in selected tropical montane forests. Negative mineralization rates indicate a net loss.

Location	Elev. [m]	Depth [cm]	KCl-extr. N NO_3-N	KCl-extr. N NH_4-N	Water-soluble N NO_3-N	Water-soluble N NH_4-N	N_{tot} [%]	Net min. $\mu\, g\, g^{-1} 14\, d^{-1}$	Net. nitr. $\mu\, g\, g^{-1} 14\, d^{-1}$
Gunung Silam,	680	0–5	-	65.9	2.9	32.3	0.06		
Malaysia[1]	870	0–5	-	43.8	2.66	24.8	0.4	?	?
Serrania de Macuira, Colombia[2]	750	0–10	0.38	12.7	-	-	0.24	3.6	0.8
Volcán Barva,	1000	0–10	4	<5	-	-	1.4	11	13
Costa Rica[3]	1500	0–10	$\lesssim$4	5	-	-	1.8	6	9
	2000	0-10	3	7	-	-	1.9	1	6
	2600	0–10	1.5	17.5	-	-	1.9	-2	3
Blue Mountains, Jamaica									
Mull[4]	1600	0–10	17	239	-	-	1.7	56	48
Mor[4]	1600	0–10	31	364	-	-	1.6	31	35
Yallahs River[6]	1300	0–10	-	-	-	-	0.68	7.2	7.8
WMull[5]	1600	0–14	-	-	26.2	61.7	-	-	-
PMull[5]	1809	0–14	10.6	235	16.2[5b]	13.8[5b]	0.7–1.1[5b]	112	5.3
MMor[5]	1824	0–5	6.2	465	17.9[5b]	14.4[5b]	1.4–1.5[5b]	-4.6	2.4
Mor[5]	1600	0–9	-	-	16.5	7.2	-	-	-
Genting, Malaysia[7]	-	0–14	2.2	0.9	-	-	0.28	9.2	3.6
	-	0–14	0.1	1.3	-	-	0.29	13.1	4.9
Mauna Loa, Hawaii[8]	1220	0–6	0	18	-	-	1.4	-12	0
	1585	0–6	0	33	-	-	1.4	-25	0
Bukit Belalong, Brunei[9]	200	0–5	5.2	-	-	-	0.36	-	10
	520	0–5	6.4	-	-	-	0.46	-	7.7
	880	0–5	4.8	-	-	-	0.57	-	11.1
Gunung Rakata, Indonesia[10]	710	0–5	1.82	30.7	-	-	0.66	10.6	8.8

Mineralization and nitrification rates are standardized to $\mu\, g\, g^{-1} 14\, d^{-1}$. [1] *Bruijnzeel et al.* [1993], *Waterloo* [1989]; [2] *Cavelier* [1988]; [3] *Marrs et al.* [1988]; [4] *Tanner* [1977a]; [5] this study, [5b] see Table 2.10; [6] *McDonald* [2000]; [7] *Chandler* [1985]; [8] *Vitousek et al.* [1988]; [9] *Pendry and Proctor* [1996b]; [10] *Hafkenscheid* [1994].

his incubation experiments were performed under relatively high temperatures (26–29 °C) in a laboratory at Kingston but there is no explanation for the even higher values found for the present PMull forest. *Vitousek et al.* [1982] reported a median net mineralization rate of 700 $mg\,N\,m^{-2}\,14\,d^{-1}$ for a series of temperate forests selected for their low N-availability. Compared with the *c.* 2500 and $-32\ mg\,N\,m^{-2}\,14\,d^{-1}$ found for the PMull and MMor forest, respectively, it can be concluded that a significant effect on plant growth is to be expected in the stunted MMor forest (see also below).

An important sink for plant available nitrogen can be denitrification or the reduction of NO_3 by denitrifiers. The fluxes of N_2O produced in this way, however, generally have a very high spatial and temporal variability [*Keller et al.*, 1983] and results of incidental experiments should be treated with caution. The present N_2O release rates (Table 9.6) are low compared to values obtained in lowland tropical ecosystems [*Keller et al.*, 1983; *Matson and Vitousek*, 1987] but comparable to rates found for montane sites in Hawaii and Mexico [*Matson and Vitousek*, 1987; *Davidson et al.*, 1993]. When considering emission of N_2O as the only indication of atmospheric nitrogen losses (therefore neglecting the release of N_2 and NO; *Firestone and Davidson* [1989]), the annual gaseous emissions of N in the study area constitute <0.9 % and <0.5 % of the annually produced NO_3-N in the PMull and MMor forest, respectively. These rates are higher than found for Hawaiian forests (0.15 % to 0.19 %; *Matson and Vitousek* [1987]) but they are too small to play a significant role in the soil nitrogen cycle.

9.4.5 Soil biotic processes and nutrient cycling

Environmental conditions

Tanner [1981] concluded from his decomposition experiments that there is too little contrast between Jamaica's Mull- and Mor-type forests in terms of leaf litter decomposition or inputs of organic material to the forest floor to explain the observed accumulation of ectorganic material on top of the mineral soils in the Mor forest. He went on to suggest that decomposition of organic material should be followed throughout the ectorganic layers (LFH-horizons) in order to gain a better understanding of the causes of mor humus accumulation. Because the lateral distance between the PMull and MMor forests was small (<30 *m*), differences in decomposition of organic material (be it at the forest floor or deeper in the ectorganic layers) cannot be explained by differences in climatic factors such as soil temperatures (*cf.* Table 9.6) although penetration of photosynthetically active radiation (PAR) through the more open canopy of the MMor forest was higher than in the PMull forest (Section 4.4.3). Similarly, changes in topsoil water tensions were more pronounced in the MMor than in the PMull forest where the soil tended to remain more moist year-round (Section 5.6.4) whereas during sunny spells MMor litter was often observed to dry rapidly. As such, although frequent wetting/drying of decomposing substrate is believed to stimulate decomposition [*Vitousek*, 1984] and CO_2 respiration rates [*Sørensen*, 1974], other factors must be more dominant in the MMor forest. Furthermore, waterlogged conditions, which cause anaerobic

conditions [*Silver et al.*, 1999], nor very low soil water contents which would both lower bio-activity and therefore decomposition rates [*Gunadi*, 1993; *Singh and Gupta*, 1977; *Tate et al.*, 1993] were never observed (Section 5.6.4). High permeability and abundant macro-pores (*cf.* Table 2.8) prevent soils from becoming saturated, even during the heaviest rain storms whereas prolonged droughts are also very rare (Section 5.6.4). Extreme soil moisture levels are therefore not likely to restrict forest floor respiration in the study forests, implying that significant differences in composition of the organic material rather than environmental contrasts lead to a different decomposition product, such as mor humus formation in the MMor forest *vs.* more complete mineralization in the PMull forest (*cf.* Table 9.4).

Substrate quality

Decomposition during the early stages of litter breakdown has often been correlated with the concentrations of N and P in the litter which reflects the microbial requirements for these nutrients [*Berg and Staaf*, 1980]. Various investigators have described the importance of nitrogen in regulating organic decay [*Coulson et al.*, 1960; *Duchaufour*, 1983]. In general, foliage and other organic residues high in nutrient concentrations (including N) tend to decay at a faster rate [*Schlesinger*, 1977]. In a comparison of two sites in northeast Queensland, *Maggs and Hewett* [1990] (Table 9.8) found that lower soil respiration rates were associated with lower nutrient concentrations (especially P and Ca) and high polyphenol concentrations in foliage as well as with high soil acidity and thicker leaves. The similarity with the Jamaican situation (Mull *vs.* Mor-type forests) is remarkable. Not only are the leaves (or leaf litter) in the Mor-type forests tougher (thicker; Table 2.4; *cf. Tanner and Kapos* [1982]) and poorer in N and K (Tables 8.7 and 8.9) but also the litter and topsoil are much more acid (Fig. 2.7 in Chapter 2). Foliar concentrations of polyphenols in the MMor were not higher than in the PMull, however, although they were in leaf litterfall (Table 8.7).

Looking at average N concentrations in mature foliage (such as used in the litterbag experiment) there was no significant difference between the Mull and Mor-type forest although distinct differences occurred between individual species (Table 9.2, see also Table 3.7). This may explain why decay rates in litterbags in the PMull forest did not become significantly higher until after one year of decomposition (Fig. 9.2). *Tanner* [1977a, b] reported gradually decreasing average concentrations of N, P, K, and Ca in foliage and leaf litter from tall Gap forest, intermediate Mull forest to stunted Mor forest in the study area and suggested that all of these elements could be limiting forest growth. Later, *Tanner* [1985] concluded from overall forest nutrient content data (aboveground biomass and trunk growth) that the impoverished character of the Mor forest is probably due to a limited supply of N and K, and possibly of Ca and P. The relations between foliar concentrations of any nutrient and forest stature, trunk growth or leaf production (litterfall), however, were less consistent than when concentrations in litter were concerned. Leaf litter in the PMull forest showed significantly higher concentrations of N and most other macro-nutrients

including Ca and K (and Al) (Table 8.7).

As demonstrated in Tables 9.10 and 9.11 amounts of readily available nutrients in water percolating through the upper part of the litter layer (L-horizon) equalled or exceeded corresponding rates of gross uptake (net uptake associated with stem growth plus small litterfall) for Ca, Mg, and K, but not for N and P. It would appear therefore that the latter two elements may be more critical to forest growth than any of the base cations [*cf.* *Tanner*, 1985] in both the PMull and the MMor forest. Now that N mineralization and nitrification rates have been determined for the two forests (Table 9.4), what are the implications for the availability of N?

Annual production of N via net mineralization and nitrification in the PMull forest amounted to *c.* 610 and 31 $kg\,ha^{-1}$ (Section 9.3.3). Adding the 5.4 $kg\,ha^{-1}\,yr^{-1}$ supplied to the forest floor via net precipitation (mineral N only) gives a total N supply of *c.* 645 $kg\,ha^{-1}\,yr^{-1}$, *i.e.* more than eleven times the estimated 55 $kg\,ha^{-1}\,yr^{-1}$ required for gross uptake (Table 9.10). The N-situation in the MMor forest is far less favourable (Table 9.11): the 4.5 $kg\,ha^{-1}\,yr^{-1}$ of (mineral) N in net precipitation is insufficient to compensate the -12.8 and 4.3 $kg\,ha^{-1}\,yr^{-1}$ lost/supplied by mineralization and nitrification, respectively, giving a net N loss of -4.0 $kg\,ha^{-1}\,yr^{-1}$. Adding the total amount of total N supplied by small litterfall (Table 9.11) gives a total N supply of 34.7 $kg\,ha^{-1}\,yr^{-1}$. This is 12 % less than the 39.4 $kg\,ha^{-1}\,yr^{-1}$ associated with gross N uptake (Table 9.11). However, this deficiency increases to more than 75 % when the presently found decomposition constant of 0.35 is applied to the nutrient flux via small litterfall (line 6 in Table 9.11). The discrepancy between estimated amounts of available and required nitrogen arguably constitutes the most direct line of evidence for N-deficiency in Mor-type forest. It should be noted however that amounts of potentially available dissolved organic nitrogen (DON) in the litter percolate were not included in these computations.

Whilst an initially equally unfavourable balance was calculated between readily available amounts of P (read: PO_4-P) in litter percolate and amounts of P required for gross uptake (Tables 9.10 and 9.11), it should be remembered that amounts of dissolved organic P (DOP) in the litter percolate were about ten times higher than amounts of PO_4-P (Table 2.12). Further work is necessary to ascertain to what extent DOP in litter percolate and soil water is potentially available for plant growth, *e.g.* via mycorrhizal mediation [*Herrera*, 1979]. The fact that concentrations of DOP decrease by about 50 % in the PMull (95 % in the WMull) and by about 20 % in the MMor forest when going from litter percolate to soil moisture in the Ah-horizon (Table 2.12) suggests that uptake of DOP may indeed take place. In any case, when the presently derived k_L values are applied to the amounts of P supplied to the forest floor by small litterfall the total inputs of P are 20 and 29 % below estimated gross uptake in the PMull and MMor, respectively (Tables 9.10 and 9.11), but the total inputs are sufficient in both forests when full decomposition is assumed. Future work should assess what fraction of the P released from litter becomes complexed by Fe- and Al-compounds [*Sanchez*, 1976] and organic matter (including phenolic compounds) in the soil and what remains available for uptake. Recent root

Table 9.10: Overview of the estimated annual nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in the PMull forest.

(A) PMull forest

	Pathways		Ca	Mg	K	P	N	Al
(1)	Net precipitation	$Tf+Sf$	13.2	5.9	44.0	0.18*	5.4*	-
(2)	Litterfall	LF	50.2	13.2	11.4†	2.9	52.9	5.2
	Idem using $k_L = 0.75^{\square}$		37.7	9.9	8.6†	2.2	39.7	3.9
(3)	Total input	$Tf+Sf+LF$	63.4	19.1	55.4	3.1	58.3	5.2
	Idem using a $k_L = 0.75^{\square}$		50.9	15.8	52.6†	2.4	45.1	3.9
(4)	N-mineralization						642	
(5)	Total input plus mineralization		63.4	19.1	55.4	3.1	700.3	5.2
(6)	Total input ($k_L = 0.75^{\square}$) plus mineralization		50.9	15.8	52.6	2.4	687	3.9
(7)	Readily available nutrients[1]	LP	66.7	29.0	108.7	1.4/0.16*	27.7/10.1*	4.9
(8)	Net uptake (immobilization in stems[2])	NU	2.6	0.5	2.3	0.11	2.3	-
(9)	Gross uptake	$LF+NU$	52.8	13.7	13.7	3.0	55.2	$\geq$5.2
(10)	Loss via drainage	D	7.7	8.6	9.1	0.24/0.08*	8.0/7.0*	1.8
(11)	Net ecosystem gain	$P+CW-D^{\ddagger}$	1.9	-6.4	-0.6	0.06*	-1.1*	-1.8

[1]nutrient flux via litter percolate, *i.e.* the nutrients arriving at the top of the rooted part of the humus/soil complex; [2]data from *Tanner* [1985]; *mineral forms only; $^{\square}$litterbag-derived k_L; † seriously underestimated because of leaching from the littertraps; ‡ minus sign indicates a net loss.

Table 9.11: Overview of the estimated annual nutrient fluxes ($kg\,ha^{-1}\,yr^{-1}$) in the MMor forest.

(B) MMor forest

	Pathways		Ca	Mg	K	P	N	Al
(1)	Net precipitation	$Tf+Sf$	12.1	6.4	33.3	0.18*	4.5*	-
(2)	Litterfall	LF	40.5	11.6	7.9†	2.2	38.6	1.5
	Idem using $k_L = 0.56^{\diamond}$		22.9	6.5	4.4†	1.2	21.6	0.8
	Idem using $k_L = 0.35^{\square}$		14.2	4.1	2.7†	0.8	13.5	0.5
(3)	Total input	$Tf+Sf+LF$	52.6	18.0	41.6	2.4	43.1	1.5
	Idem using $k_L = 0.56^{\diamond}$		35.0	12.9	37.7	1.4	26.1	0.8
	Idem using $k_L = 0.35^{\square}$		26.2	10.5	36.0†	1.6	18.0	0.8
(4)	N-mineralization						-8.4	
(5)	Total input plus mineralization		52.6	18.0	41.6	2.4	34.7	1.5
(6)	Total input ($k_L = 0.35$) plus mineralization		26.2	10.50	36.0	1.6	9.6	0.8
(7)	Readily available nutrients[1]	LP	39.3	22.1	68.3	0.95/0.19*	19.3/4.1*	1.9
(8)	Net uptake (immobilization in stems[2])	NU	0.7	0.3	0.5	0.06	0.8	-
(9)	Gross uptake	$LF+NU$	41.2	11.9	8.4	2.25	39.4	$\geq$1.5
(10)	Loss via drainage	D	2.1	7.6	6.9	0.33/0.07*	7.1/4.7*	6.3
(11)	Net ecosystem gain	$P+CW-D^{\ddagger}$	8.4	-5.0	2.0	0.09*	1.6*	-6.3

[1]nutrient flux via litter percolate, *i.e.* the nutrients arriving at the top of the rooted part of the humus/soil complex; [2]data from *Tanner* [1985]; $^{\diamond}$litterfall divided by litter standing crop (*cf.* Chapter 8); $^{\square}$litterbag-derived k_L; *mineral forms only; †seriously underestimated because of leaching from the littertraps; ‡ minus sign indicates a net loss.

ingrowth experiments in the Mor Ridge forest [*Stewart*, 1999], however, suggest N and P to be equally limiting.

Now that various aspects of the nutrient dynamics if the PMull and MMor forest have been quantified and limiting factors have been identified (notably N in the MMor), the nutrient data will be combined with the pedological, climatic, hydrological and plant physiological information given in chapters 2–6 in the next concluding chapter which will present an emerging view of the causes of forest stunting of some of these upper montane forests.

10

FOREST STUNTING IN THE BLUE MOUNTAINS OF JAMAICA: AN EMERGING VIEW

10.1 SUMMARY OF THE PRESENT FINDINGS

In Chapter 1 a number of hypotheses that have been advanced over the years to explain forest stunting on wet tropical mountains were introduced briefly. This section reviews the respective hypotheses in the light of the present findings. Remaining questions and suggestions for further research are formulated in Section 10.3.

10.1.1 CLIMATIC CONDITIONS AND FOREST STATURE

Exposure to high wind speeds has been forwarded as a possible cause of forest stunting on tropical mountains, especially on exposed summits and ridges away from the equator [*Howard*, 1968; *Jaffe*, 1980; *Lawton*, 1982; *Sugden*, 1986] but winds at equatorial latitudes do not seem to play an important role [*Proctor et al.*, 1988; *Hafkenscheid*, 1994; *Pendry and Proctor*, 1996b]. Although the present study area is situated in the trade wind belt (*i.e.* outside the equatorial zone of low winds) the general wind speeds measured at the freely exposed summit of Bellevue Peak (1849 m a.s.l.) proved to be modest (average over 1995: 4.1 $m\,s^{-1}$; maximum recorded wind speed: 16.4 $m\,s^{-1}$; Section 4.4.3). Furthermore, there are no indications that hurricanes (which pass Jamaica roughly once every 15 years) cause greater selective damage to the stunted forest varieties than to the taller forests [*Bellingham*, 1993]. In short, strong winds can be rejected as an important factor governing the occurrence of stunted forests in the study area.

Incidental drought has been advocated as a possible mechanism of montane forest stunting, especially on shallow ridge-top soils [*Lowry et al.*, 1973; *Van Steenis*, 1972; *Werner*, 1988]. As shown in Section 2.3.3, amounts of plant available water (PAW) in the upper 50 cm of the soil underlying tall 'well-developed' Mull forest (WMull) were only marginally larger than in the most stunted of the four forests considered in the present study, viz. the Mor forest (166 mm *vs.* 137 mm). Although the nearly equally stunted MMor

forest had the lowest PAW (128 *mm*), a ranking of the four forests according to their PAW values did not parallel the ranking based on stature. Also, although soil water tensions in 1995 in the MMor forest were higher than in the nearly adjacent taller PMull forest due to the coarser texture of the MMor soil (Table 2.8), the critical values of -0.1 *MPa* ($pF = 3$: the level where water uptake may start to fall below the potential rate) or -1.58 *MPa* ($pF = 4.2$: permanent wilting point) were never attained in either forest (*cf.* Figs. 5.5 and 5.6). Neither were there any indications of disproportionately higher leaf litter production during rainless periods in the stunted MMor forest compared to the PMull forest (*cf.* Figs. 8.1 and 8.2). Furthermore, observations by *Kapos and Tanner* [1985] in 1974–1975 in the study area using gravimetric methods indicated that the soil below tall Mull forest became drier than below stunted Mor forest. Finally, a drought simulation exercise (Section 5.5.4) showed that it would take two (Ah- and Bh-horizons; 0–10 *cm*) to eight (Bw-horizon; 10–35 *cm*) rainless weeks to reach soil water tensions of -0.1 *MPa*, and 6–12 weeks for the Ah- and Bh-layers to reach permanent wilting point in the MMor forest. The complete drying out of the Bw-horizon would even take more than 30 weeks. The corresponding dry periods required in the case of the PMull forest soil were 5–6 weeks (Ah–Bh horizons; 0–40 *cm*) to eight weeks (Bw1-horizon; 40–65 *cm*) to reach a value of -0.1 *MPa vs.* 17–34 weeks to reach wilting point (depending on the soil horizon). Although rainless periods of 30 and 39 days have occurred in the past at nearby Cinchona these would not have been enough to induce serious soil water stress below 10 *cm* depth in the MMor forest. Also, rainfall at the study sites is believed to be *c.* 25 % higher than at Cinchona whereas, in addition, contributions by cloud water interception -however modest- should be taken into account as well (*cf.* Section 4.4.2). In conclusion, drought seems to play a minor role at best as a factor causing stunted forest growth in the study area.

Waterlogging and subsequent root-anoxia have also been advanced as an explanation for the development of stunted montane forests [*Silver and Vogt*, 1993; *Silver et al.*, 1999]. Indeed, most observations of soil water dynamics in upper montane forests indicate wet to very wet soil conditions (presumably as a result of additional horizontal precipitation inputs and low evaporation [*Bruijnzeel and Proctor*, 1995]). However, the present findings on soil physical properties leave little chance for fully saturated soil conditions to develop in the study forests. Both saturated hydraulic conductivity and porosity of the topsoils are high and, more importantly, both are higher in the soil underlying the stunted MMor forest than in the taller PMull forest (Table 2.8). Also, during exceptionally heavy rainfall (>1200 *mm* in 5 days in February 1996), the soils in the study forests never became waterlogged. These observations are in line with those of *Kapos and Tanner* [1985] during 1974–1975. Summarizing, (excessive) waterlogging is not considered a factor of any significance governing forest stature in the study area.

Reduced air and leaf temperatures associated with reduced radiation inputs

have been suggested to cause low-statured forest on wet tropical mountains [*Grubb*, 1977]. However, air temperatures in the study area as recorded at 1849 m a.s.l. were not particularly low. Average 24-h and daytime (06:00 – 18:00 h) above-canopy temperatures were estimated at 16 and 17 $^{\circ}C$ (Section 4.4.3). On sunny days, air temperature remained above 20 $^{\circ}C$ for approximately 5 h whereas under cloudy conditions it remained at a constant 16 $^{\circ}C$ throughout the day (*cf.* Fig. 4.4C). Furthermore, *Kapos and Tanner* [1985] showed that the differences between leaf and air temperatures in the study area were very small. As such, it is very unlikely that leaf temperatures in Jamaica's stunted forests would become so low as to restrict photosynthesis and/or respiration.

A reduction in solar radiation inputs due to persistent fog and low cloud has been suggested to potentially have an adverse effect on plant photosynthesis [*Grubb*, 1977]. Compared to lowland conditions the estimated reduction in annual radiation load at *c.* 1600 m a.s.l. in the study area is approximately 16 % [*Aylett*, 1985] which is modest compared to the 15–50 % reported for tropical montane forests elsewhere [*Bruijnzeel and Veneklaas*, 1998]. More importantly, both stunted and taller-statured forests in the study area receive an average radiation load of 13.8 $MJ\,m^{-2}$ (Section 4.4.3). Similar radiation loads at lower elevations do not prevent the development of relatively tall forest elsewhere, *e.g.* in East Malaysia [*Bruijnzeel et al.*, 1993] and in eastern Puerto Rico [*Holwerda*, 1997] (Section 4.5.1). As such, low radiation *per se* cannot play an important role in governing forest stature in the study area. More specifically, using the threshold value for light saturated photosynthesis proposed by *Aylett* [1985] it was demonstrated (Section 4.4.3) that photosynthetically active radiation levels in the study area remained above 250 Wm^{-2} (500 $\mu mol\,m^{-2}\,s^{-1}$) for 52 % of all day-time hours (06:00 – 18:00 h) and for 80 % of the time that light was potentially non-limiting (on average between 07:30 and 17:10 h). Furthermore, rates of maximum photosynthesis A_{max} (which are believed to be a good indication of the integrated, long-term CO_2 assimilation [*Zotz and Winter*, 1993; *Field*, 1988]) were not systematically higher in individual tall-statured Mull forest trees than in the short-statured Mor forest (Table 6.3). Plot-averaged values (Section 6.3.1) of A_{max} per unit of leaf *mass* (A^m_{max}) paralleled the ranking of the four forest types based on their stature (WMull>PMull>MMor>Mor) but no such trend was found when rates were expressed per unit leaf area (A^a_{max}; Table 6.4).

Approximate estimates of forest productive photosynthetic capacity at stand level suggested net carbon assimilation totals of 3.3, 4.1, 4.0, and 5.6 $kg\,C\,m^{-2}\,yr^{-1}$ for the Mor, MMor, PMull, and WMull forest, respectively (Section 6.4.4). Although these values must be regarded with considerable caution, at least the highest and lowest values are indeed associated with the tallest (WMull) and shortest (Mor) forest types, respectively. Because the radiation climate is similar for the tall- and short-statured forests alike, these differences in carbon gain between forests reflect differences in LAI only (*cf.* Section 2.3.1). Summarizing, the contrasts in stature between the respective forest types are not caused by differences in photosynthetic capacity at the leaf

level, nor by persistently low radiation levels.

Reduced atmospheric evaporative demands suppressing rates of water and nutrient uptake have also been advocated as a possible explanation of forest stunting [*Odum*, 1970; *Weaver et al.*, 1973; *Ash*, 1987]. This idea has already been rejected on theoretical plant physiological grounds [*Grubb*, 1977] and the present climatic observations do not support it either. First, the average rate of open-water evaporation E_0 (a convenient measure to characterize overall evaporative demand) in the study area is relatively high (3.0 $mm\,d^{-1}$; Section 4.4.3), especially when considering that it was obtained for an elevation of 1849 m a.s.l.. Furthermore, the estimated rates of forest water uptake E_t (*i.e.* 510 and 620 $mm\,yr^{-1}$ for the MMor and PMull forest, respectively; Section 5.5.3) are at the low end of the range reported for tall montane rain forests that are little affected by fog and low cloud, but they greatly exceed the 250–310 $mm\,yr^{-1}$ associated with short-statured 'mossy' forests subject to frequent fog incidence [*Bruijnzeel and Proctor*, 1995]. These high transpiration rates become even more pronounced when expressed as a ratio to E_0. The presently obtained E_t/E_0 ratios, 0.5 for the Mor forest and 0.6 for the PMull forest (Section 5.6.2, page 120), are far above the 0.22–0.25 reported for short-statured summit forests at low elevation but they are very similar to the values obtained for tall montane forests experiencing little to no cloud (0.47–0.56) [*Bruijnzeel and Proctor*, 1995]. In combination with the fact that cloud water interception by the study forests is minor (Section 4.4.2), these findings suggest that the present forest can perhaps not be regarded as 'true' cloud forests, *i.e.* forests characterized by both high cloud water interception and low transpiration [*cf. Stadtmüller*, 1987].

In conclusion, the present meteorological observations as conducted at 1849 m a.s.l. in the upper montane forest zone of Jamaica provide no evidence for significantly lowered plant production potential, either through reduced leaf temperatures, intrinsically low levels of photosynthetically active radiation (PAR) or low atmospheric evaporative demands. Moreover, if (one of) these climatic factors would be important in governing forest stature, this would apply equally to both tall-statured and stunted forest communities alike and, therefore, would not be able to explain the observed physiognomic contrasts. Furthermore, neither excessive soil saturation or root anaerobiosis, nor high cloud water incidence and prolonged canopy wetness, nor prolonged drought or (selective) damage by strong winds can be considered to play an important role in determining forest stature in the Blue Mountains of Jamaica. Because climatic and hydrological conditions thus do not explain the observed contrasts in forest physiognomy, attention will be focussed on edaphic conditions in the following section.

10.1.2 Edaphic conditions, nutrient dynamics and forest stature

Limited nutrient supply has been considered an important potential explanation of montane forest stunting in many cases [*Tanner et al.*, 1998], either in

relation to overall low fertility of the substrate [*Van Steenis*, 1972], reduced decomposition and mineralization rates [*Grubb*, 1977; *Marrs et al.*, 1988], or extreme acidity that might hamper uptake of key nutrients [*Tanner*, 1977a]. Outside the context of tropical montane forests, extreme acidity is known to induce aluminium toxicity and hamper plant productivity [*Sanchez*, 1976; *Northup et al.*, 1995]. The respective hypotheses are examined in the following section in the light of the new results from the Jamaican sites.

Overall low soil fertility

Previous work in the study area by *Tanner* [1977a, b] indicated gradually decreasing average concentrations of key elements (N, P, K, Ca) in foliage and leaf litterfall from tall 'Gap' forest via intermediate Mull forest to stunted Mor forest, suggesting that all of these elements could be limiting forest growth. Later, *Tanner* [1980b, 1985] concluded from stem growth and overall nutrient contents of the above-ground biomass that the stunted character of the Mor forest is probably due to a limited supply of N and K, and possibly of Ca and P. More recently, *Stewart* [1999] suggested N-deficiency for intermediate-statured Mull forest and N+P-deficiency for Mor forest on the basis of root ingrowth experiments.

The present results for foliar chemistry show a less consistent pattern. Elemental concentrations in mature leaves were not significantly higher in the PMull than in the MMor forest (Tables 3.7 and 3.8) and, with the exception of K, elemental concentrations in young and old leaves did not parallel the ranking of the four forests based on stature (Fig. 3.3). Nevertheless, concentrations of N, P, Ca and K in leaf litter from the PMull forest were significantly higher than for the MMor forest (Table 8.4). One could argue, therefore, that there is a (weak) relationship between forest stature and the nutrient status of the forest itself. However, as will be demonstrated below, neither the contrasts in stature nor in foliar/litter chemistry can be related to intrinsically low soil fertility. Firstly, amounts of $BaCl_2$-extractable base cations, ammonium-N, and total-N present in the top 50 *cm* of the soils were not consistently higher in Mull-type forest than in the more stunted Mor-type forests (Table 2.11). In fact, Na, Mg and oxalate-extractable P were (much) higher in the Mor and MMor forests, whereas amounts of exchangeable K, Ca, and NH_4 were even highest in the most 'restricted' forest, the Mor (Table 2.11). It must be concluded that there is no direct relationship between forest stature and amounts of extractable elements in the soil. Secondly, the annual atmospheric nutrient inputs to the respective forests are such that low soil fertility alone cannot provide an explanation for the observed contrasts in stature. Atmospheric nutrient inputs to the stunted MMor forest were higher than for the taller PMull forest, basically as a result of the contrasts in the interception of relatively nutrient-rich cloud water (Tables 7.2 and 7.4). In addition, compared to annual atmospheric inputs to montane tropical forests elsewhere, the Jamaican sites occupy an intermediate position between the very high inputs reported for only 2–3 *m* tall 'elfin' cloud forest in eastern Puerto Rico and the relatively low inputs to a 30–40 *m* tall lower montane forest at 2500 *m* a.s.l. in Papua

New Guinea (Table 7.7), suggesting that atmospheric deposition *per se* is not related at all to forest stature. Finally, although no data are available for the PMull and MMor forests on the amounts of nutrients incorporated annually in stem increment ('net uptake'), the comparison of such estimates for the WMull and Mor forests [*Tanner*, 1985] with corresponding amounts brought in via atmospheric deposition [*cf. Bruijnzeel*, 1989a] shows that atmospheric nutrient inputs far exceed the net uptake (Tables 7.10 and 7.11). As such, one may conclude that forest stature is not controlled by atmospheric nutrient inputs alone, neither in the study area nor in montane forests elsewhere.

Forest nutrient budgets

Nutrient fluxes associated with the respective water- and litter-bound pathways have been summarized in Tables 7.10 and 9.10 (PMull forest) and Tables 7.11 and 9.11 (MMor forest). The present synthesis will concentrate on the essentials, using the summary diagrams shown in Figs. 10.1 and 10.2 in addition to the tables.

On an ecosystem basis, both the PMull and the MMor forest were losing net amounts of Si, Mg, Na, Al, and Fe, as well as NO_3-N, total N and total P. Also, a slight net loss was obtained for K in the case of the PMull forest, but K apparently accumulated in the MMor forest. Net ecosystem accumulations were also observed for Ca, NH_4-N and PO_4-P.

To highlight potentially limiting nutrients, or differences between sites, it is often more illustrative to contrast amount of nutrients arriving at the top of the rooted part of the soil in litter percolate (LP), or in net precipitation (NP, throughfall plus stemflow) plus those released by litter decomposition and mineralization, against corresponding amounts taken up by the forest and lost in drainage water (D). Net uptake (NU) of a nutrient is defined in this respect as the uptake associated with annual stem increment whereas gross uptake (GU) refers to the annual production of small litterfall (LF) (leaves, reproductive parts, twigs). Its is recognized that this definition of gross uptake represents an underestimate because it does not include the nutrient requirements associated with increments in below-ground biomass (roots) or large branches.

Before addressing Figs. 10.1 and 10.2 a few comments are in order. As discussed more fully in Section 8.5.4, the annual fluxes of K in small litterfall in both the PMull and MMor forest may have been underestimated by as much as 60–80 % due to problems with leaching from the littertraps before sample collection. As a result, estimates of GU for K are underestimated accordingly. In an attempt to correct for this, the difference between amounts of K carried in litter percolate (LP) and net precipitation (NP) were added to the amounts measured in LF to give the corrected K flux in litterfall (LF^*). Also, considerable quantities of K were leached from the canopy in both forests (*cf.* Table 7.5). It could be argued that the amounts involved (termed 'net canopy effect' (NCE) in Fig. 10.1) should be added to the 'regular' estimate of GU. Thus, the corrected gross uptake of K (GU^*) becomes:

$$GU^* = NU + LF^* + NCE \tag{10.1}$$

Unfortunately, the consequence of addressing the K-leaching problem using

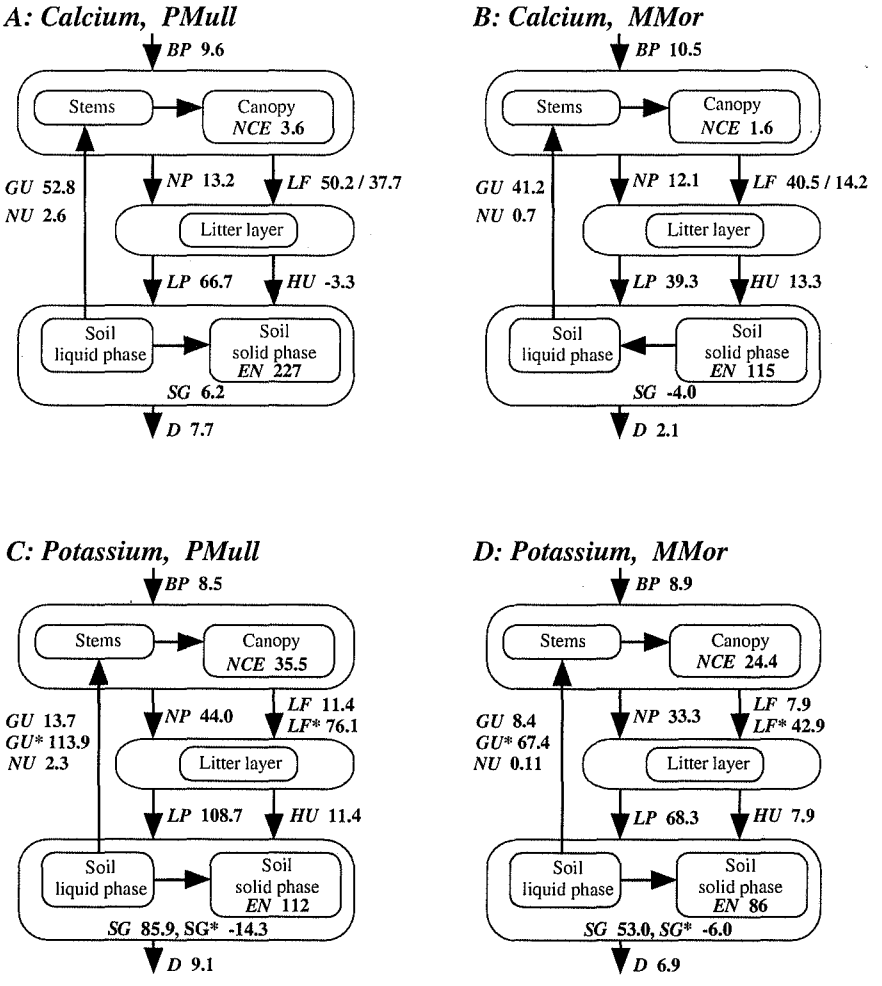

Figure 10.1: Simplified diagrams depicting the cycling of Ca and K in the PMull (left) and MMor (right) forests. All values are $kg\,ha^{-1}\,yr^{-1}$, except for EN which is in $kg\,ha^{-1}$. The respective fluxes are: BP, nutrient input via bulk precipitation (P+CW); NP, net precipitation (Tf+Sf); NCE, net canopy effect (leaching or absorption; *i.e.* (Tf+Sf)−(P+CW)); LF, litterfall; LF^*, corrected for leaching of K from the littertraps (LF+LP−NP); LP, litter percolate; HU, humification (LF+NP−LP); NU, net uptake (stem increment); GU, gross uptake (LF+NU); GU^*, gross uptake of K (LF^*+NU+NCE); D, drainage; SG, net gain in mineral soil (LP−D−GU/GU^*; negative values for SG denote a decrease in storage); EN, exchangeable nutrients present in the top 50 *cm* of soil (*cf.* Table 2.11). Large branches- and tree-fall have not been taken into consideration. The second values for LF represent annual inputs via litterfall with decomposition taken into account, *i.e.* $LF \times k_L$, with $k_L = 0.75$ for PMull and $k_L = 0.35$ for MMor litterfall.

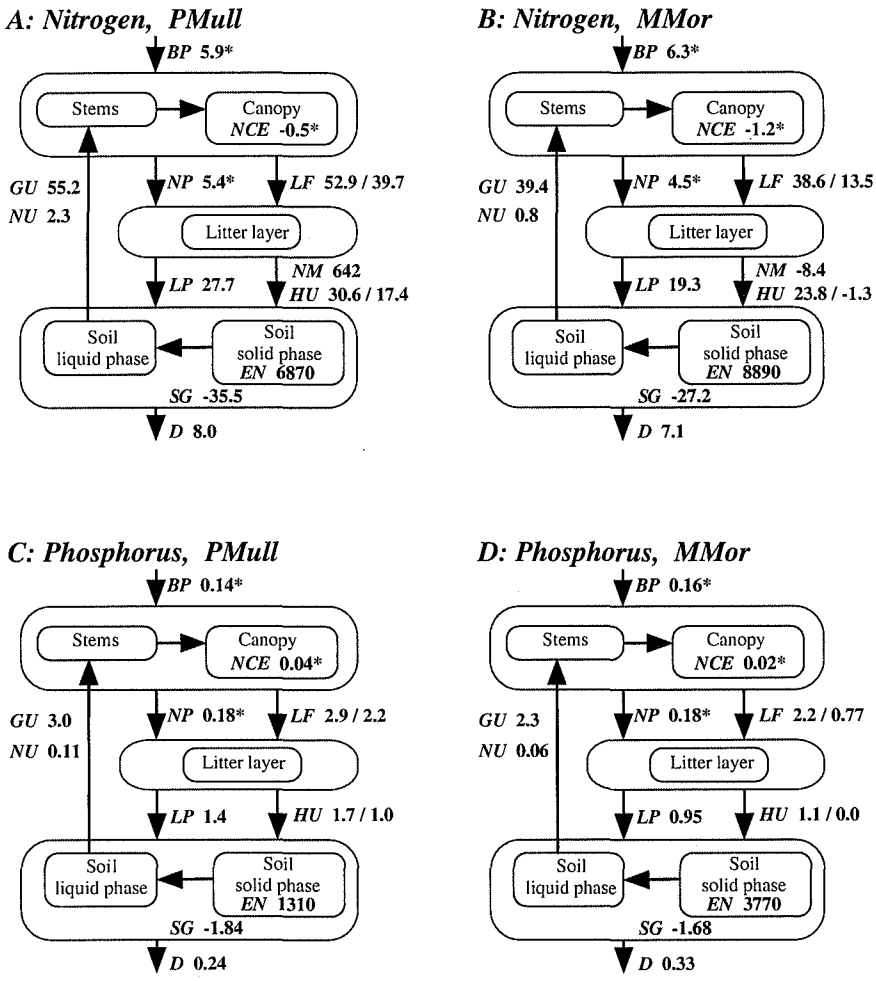

Figure 10.2: Simplified diagrams depicting the cycling of N and P in the PMull (left) and MMor (right) forests. All values are $kg\,ha^{-1}\,yr^{-1}$, except for EN which is in $kg\,ha^{-1}$. Values marked * denote inorganic forms only. The respective fluxes are: BP, nutrient input via bulk precipitation (P+CW); NP, net precipitation (Tf+Sf); NCE, net canopy effect (leaching or absorption; *i.e.* (Tf+Sf)−(P+CW)); LF, litterfall; LP, litter percolate; NM, net mineralization ($kg\,ha^{-1}\,yr^{-1}$; *cf.* Section 9.3.3); HU, humification (LF+NP−LP); NU, net uptake (stem increment); GU, gross uptake (LF+NU); D, drainage; SG, net gain in mineral soil (LP−D−GU; negative values for SG denote a decrease in storage); EN, total N and oxalate-extractable P in the top 50 cm of soil (*cf.* Table 2.11). Large branches- and tree-fall have not been taken into consideration. The second values for LF represent annual inputs via litterfall with decomposition taken into account, *i.e.* $LF \times k_L$, with $k_L = 0.75$ for PMull and $k_L = 0.35$ for MMor litterfall.

such a budget approach is that few conclusions can be drawn anymore with respect to the soil K-budget (Fig. 10.1). Finally, because not all of the fine litterfall is decomposed within a single year, estimates of the amounts of nutrients released annually by litter decomposition in Figs. 10.1 and 10.2 were made by multiplying LF times the average decomposition constants derived for the respective forests ($k_L = 0.75$ for the PMull and $k_L = 0.35$ for the MMor forest; Section 9.3.1). No such correction was applied, however, in the case of K given the high mobility of this element.

A comparison of annual amounts of nutrients added to the soil in litter percolate LP with corresponding amounts of gross uptake GU and eventual losses in deep drainage D in the PMull and MMor forests yields the following (Figs. 10.1A,C and Table 9.10): additions of Ca, Mg and (presumably) K in LP alone are already sufficient to cover the respective uptake requirements, even after taking losses via drainage D into account. As for N and P (Fig. 10.2; Table 9.11), the annual gross uptake exceeded additions via litter percolate by more than two times. Because it is unknown to what extent the dissolved organic forms of N and P in LP are readily available for uptake, the actual discrepancy is likely to be even larger. However, the previous comparison did not include any contributions by decomposing litter. Because some of the nutrients contained in the litter percolate derive from litter decomposition, a more objective picture may be obtained when the amounts of nutrients released by decomposition are added to the corresponding amounts in net precipitation NP rather than litter percolate LP. Applying the latter approach to the PMull forest again showed annual additions of Mg and K to be sufficient to cover corresponding rates of gross uptake. Conversely, a deficiency of *c.* 20 % of GU was obtained for Ca, N, and P in this way. For N, this deficiency is again apparent only because the calculation did not include the large amounts of N generated via mineralization. The latter proved to be 11 times the annual gross uptake (Table 9.4). This leaves P as the only element possibly limiting productivity in the PMull forest.

Turning to the more stunted MMor forest (Fig. 10.1B,D and Table 9.11), solute inputs of Mg in litter percolate exceeded the sum of gross uptake and losses via drainage but fell short by about 10 % in the case of Ca and K. Amounts in litter percolate were sufficient, however, to meet gross uptake of K and almost so (95 %) in the case of Ca. As noted previously for the PMull forest as well, additions of total N and total P in LP in the MMor forest only made up less than half (42 % and 37 %, respectively) of the totals taken up and lost via drainage. The latter figures rose to 49 % and 41 % when only the requirements for GU were considered (Table 9.11). Repeating the exercise on the basis of the amounts of nutrients delivered annually in net precipitation NP and decomposition litter ($LF \times k_L$) gave an even less favourable picture for the MMor forest: only additions of K were sufficient to meet the requirements associated with gross uptake, let alone to compensate losses in drainage as well. Annual additions Mg, Ca, N and P contributed 88 %, 64 %, 46 % and 43 % of corresponding amounts required for gross uptake (Table 9.11). Unlike the PMull forest, where the apparent shortage of N inferred from similar calculations was more than compensated for by contributions via

N-mineralization, the nitrogen limitation in the MMor forest increased to over 75 % of gross uptake because of a negative N-mineralization (*i.e.* a net loss of $-8.4\ kg\,ha^{-1}\,yr^{-1}$; Section 9.3.3). The discrepancy between the (admittedly somewhat crudely) estimated amounts of N (and P) added annually to the soil and those required for uptake (*GU*) arguably constitutes the most direct line of evidence for N- (and P-) deficiency in the MMor forest, whereas the data suggest Ca to be critical as well (*cf.* Fig. 10.1B and Table 9.11). We will come back to the causes of the slow decomposition and net mineralization loss in the MMor forest in the section on the role of phenolic compounds (Section 10.1.3).

Summarizing: (i) There appears to be no direct relationship between the stature of the forest, foliar/litter chemistry and amounts of $BaCl_2$-extractable nutrients in the soils underlying the Jamaican forests; (ii) A comparison of amounts of nutrients added annually to the soil with corresponding amounts associated with gross uptake suggests P to be the element in shortest supply in the PMull forest, and P, and above all N, in the MMor forest whereas Ca may be critical in the MMor forest as well. However, because amounts of extractable Ca, P and NH_4-N were highest in the soil of the most stunted forest (Mor forest; Table 2.11), these apparent deficiencies cannot be attributed directly to intrinsically low soil fertility. Also, the degree of inferred P-deficiency for both forests is similar, suggesting that shortage of P is not the discerning factor between the two forests. It would seem, therefore, that, apart from the lack of NO_3-N generated by mineralization and nitrification in the MMor forest (Table 9.4), a *restriction of tree nutrient uptake ability rather than the presence of nutrients per se* is the key factor governing forest stature in the study area. This aspect will be examined more closely in the next section.

10.1.3 Forest nutrient uptake ability

As demonstrated in the previous section it is likely that with the possible exception of NO_3-N the uptake of available nutrients in the more stunted forest is limited somehow. Previously, *Tanner* [1977a] proposed that K-uptake in the Mor forest might be hampered by the extreme acidity of the site whereas *Bruijnzeel et al.* [1993] suggested that high concentrations of polyphenols in litter and topsoil could be important in this respect as well.

The decreasing concentrations of N, K, Ca, and P in foliage and leaf litter from tall-statured Gap forest, via intermediate-statured Mull to stunted Mor forest found by *Tanner* [1977a] were paralleled by the present foliar data for K only, but most other elements (including N, P and other cations) showed a far less consistent trend (Fig. 3.3, Table 3.8). Concentrations of K in leaves of all age classes were generally $<2.5\ mg\,g^{-1}$ in the PMull, MMor and Mor forests, but not in the WMull forest (Table 3.2). Based on the nutritional criteria of *Drechsel and Zech* [1991] such low values are typical for tropical forests suffering from potassium deficiency. In addition, although somewhat higher than in foliar tissue, concentrations of K in small roots also follows a trend parallel to that for stature (Table 3.5, Fig. 3.4). However, these decreasing K

concentrations in foliage, litter and fine roots with decreasing forest stature are apparently not related to amounts of $BaCl_2$-extractable K in the top 50 *cm* of the soils (highest in the Mor, Table 2.11), or to amounts of K in litter percolate or water extracted from the Ah-horizons (again high in the Mor, Tables 2.12 and 2.13). Because the increase in soil acidity with decreasing forest stature is the primary edaphic factor that distinguishes the respective forest types in the study area (Table 2.10), it is tempting to relate these patterns for K to those observed for pH [*cf. Tanner*, 1977a]. The foliar K-deficiency in the Mor-type forests may be related to the high concentrations of Al^{3+} in topsoil water which proved to be 10 times higher in Mor-type Ah-horizons than in Mull-type Ah-horizons (Table 2.16; Fig. 2.9). High levels of Al^{3+} have shown to be capable of blocking transport channels in root cell plasmatic membranes, thereby limiting the uptake of K^+ [*Kochian*, 1995; *Lüttge*, 1997]. Interestingly, concentrations of both K *and* Al in leaves (Fig. 3.3) and small roots (Fig. 3.4) increased with forest stature (and decreasing acidity). It would seem, therefore, that the uptake of K is hampered under Mor-type edaphic conditions, but also that the trees are capable of excluding Al under acid conditions (see also below).

Phosphorus
In addition to the seemingly deficient levels of K, foliar and litter concentrations of P also fall below the optimum concentration of 0.1 $mg\,g^{-1}$ or larger suggested by [*Drechsel and Zech*, 1991]. Comparison of average foliar P levels in the four forests (Table 3.8) with stocks of oxalate-extractable P in the soils (Table 2.11) suggests that the former does not reflect the latter, although the lowest values for both foliar and soil P were obtained for the WMull forest. Such lack of correlation not only questions the idea that foliar nutrient concentrations may provide information on the overall nutritional status of a forest [*cf. Drechsel and Zech*, 1991], but once again underscores the observations made earlier that at least some of the apparent nutrient deficiencies in the study forests relate to an inability of the trees to take up available nutrients rather than reflect reserves in the soil *per se* (*cf.* Section 10.1.2). *Lüttge* [1997] suggested that, besides K, also the availability of P to leaves may be reduced by high concentrations of Al because the latter have been shown to precipitate poorly soluble $Al_2(PO_4)_3$ in the apoplasts of the roots, thereby hampering further distribution of P in the plant. However, no such mechanism appears to be at work in the study area given the presently found concentrations of Al and P in the small roots (Table 3.5) and foliage (Table 3.8) in the respective forests. Finally, and as indicated earlier, although the nutrient budget approach suggested a P-deficiency for both the PMull and MMor forests, the relative discrepancies in inputs via LP (or $NP{+}LF$) and gross uptake GU were very similar for the two forests (Section 10.1.2). Summarizing, the available evidence suggests that, unlike for N, differences in soil reserves or cycling of P cannot explain the observed inter-site contrasts in forest stature.

Aluminium toxicity
Another marked contrast between the stunted Mor-type forests and the tall-

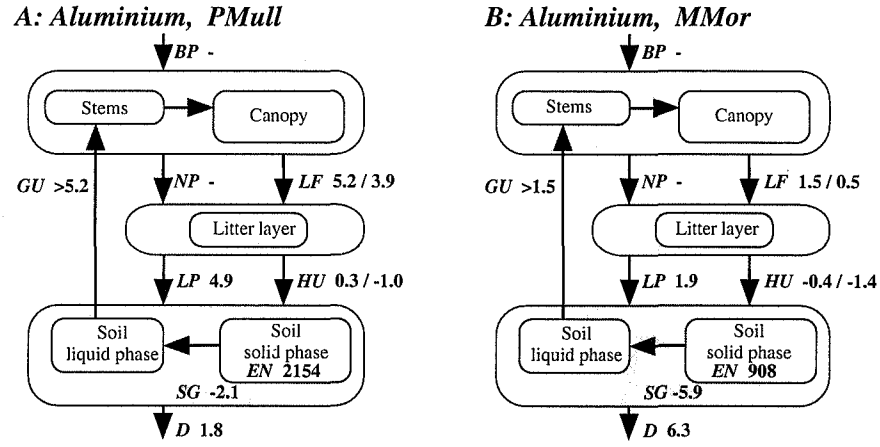

Figure 10.3: Simplified diagrams depicting the cycling of Al in the PMull (left) and MMor (right) forests. All values are $kg\,ha^{-1}\,yr^{-1}$, except for EN which is in $kg\,ha^{-1}$. The respective fluxes are: BP, nutrient input via bulk precipitation (P+CW); NP, net precipitation (Tf+Sf); LF, litterfall; LP, litter percolate; HU, humification (LF+NP−LP); GU, gross uptake (LF plus an unknown quantity of Al incorporated in stem increment); D, drainage; SG, net gain in mineral soil (LP−D−GU; negative values for SG denote a decrease in storage); EN, exchangeable Al present in the top 50 cm of soil (*cf.* Table 2.11). Large branches- and tree-fall have not been taken into consideration. The second values for LF represent annual inputs via litterfall with decomposition taken into account, *i.e.* $LF \times k_L$, with $k_L = 0.75$ for PMull and $k_L = 0.35$ for MMor litterfall.

statured WMull forest concerns that for 'free' Al^{3+} in the (top) soil moisture (see above; *cf.* Fig. 2.9). Based on criteria for Al toxicity proposed by *Cronan and Grigal* [1995] and the fact that the high concentrations were observed year-round rather than occasionally, there is supposedly > 90 % chance that the roots of the trees in the Mor and MMor forests are subject to toxic levels of Al^{3+} (*cf.* Section 2.4.4). Injuries to the root system caused by high Al^{3+} primarily concern the root apex [*Roy et al.*, 1988]. No such observations have been made yet at the study sites to confirm the validity of this contention (*cf.* Section 10.3).

Although topsoil moisture showed decreasing concentrations of Al^{3+} and increasing Ca^{2+}/Al^{3+} ratios towards the tall-statured WMull forest, values for small roots and foliage showed an opposite trend (Tables 3.5 and 3.8). Also, Al concentrations in mature Mor leaves were not significantly higher than in PMull leaves (Table 3.8) but concentrations in freshly fallen litter were (much) higher in both the WMull (Fig. 3.3) and PMull forests (Fig. 8.3). In fact, concentrations of Al in leaf litter and fluxes in total litterfall in the PMull were roughly four times those in the MMor forest (Table 8.7). However, none of the analyzed tree species in any of the four forests showed foliar Al concentrations in excess of 1000 $\mu g\,g^{-1}$ (which is an accepted criterion to identify Al-accumulating species [*Werner*, 1988]). Based on the data

collected in this study it is likely that the Mull-type forests basically apply an Al-immobilization strategy involving the deposition of Al in cell walls and vacuoles prior to abscission where it cannot damage metabolism [*cf. Cuenca et al.*, 1990]. The stunted Mor forests, on the other hand, seem unable to do this and, apparently, rely on an exclusion strategy. As will be argued below, this exclusion strategy probably involves the formation of strong Al-complexing compounds, including polyphenols. Further work is needed to evaluate the underlying cause(s) for the development of the different strategies on Mull and Mor soils (*cf.* Section 10.3).

The role of phenolic compounds

Phenolic compounds (including tannins) are known to interfere with a variety of ecological and soil chemical processes [*Kuiters*, 1990]. Organic acids and phenolic compounds have been reported to form strong complexes with Al^{3+}, thereby reducing its toxicity. Such a mechanism may operate in the Mor-type forests where concentrations of phenols in litter percolate and soil water extracted from the Ah-horizons were distinctly higher than in the Mull-type forests (Table 2.12). However, whilst the high concentrations of polyphenols in Mor-type *soil water* were indeed matched by (very) high concentrations of Al^{3+} (Fig. 2.9), the very similar Al^{3+} concentrations in the *litter percolates* of the WMull and Mor forests (Fig. 2.9) were accompanied by widely different phenol concentrations (Table 2.12). As such, the latter must be influenced by a factor other than Al^{3+}. High polyphenol concentrations in leaf litter have also been suggested to be related to N-deficiency [*Horner et al.*, 1988; *Bruijnzeel et al.*, 1993]. However, although the MMor forest was shown to be seriously deficient in N (gross uptake *GU* exceeded additions via net precipitation, litterfall and mineralization by 75 % (Section 10.1.2; *cf. Tanner et al.* [1990]; *Stewart* [1999])), neither concentrations of phenols in live foliage (Table 3.8) and small roots (Table 3.5) nor those in leaf fall (Table 8.4) were significantly higher in the (M)Mor forest than in the (P)Mull forest. Also, foliar concentrations of phenols correlated poorly with concentrations of N (Fig. 3.5). Furthermore, the relative rankings of the four forests according to phenol concentrations in small roots and mature leaves did not parallel that for forest stature (Table 3.14). Such findings suggest that the relatively high concentrations of phenols in the foliage and leaf litter of the Jamaican forests (especially in the Mor-type forests) compared to other montane tropical forests (Table 3.13) are caused by (an)other factor(s) than just low N. Interestingly, the rankings of the forests based on concentrations of Al^{3+}, phenols, and DON (dissolved organic N) in topsoil water are the same (highest in Mor, lowest in WMull) whereas those for NO_3^-, NH_4^+ and pH all showed a steady decline from WMull to Mor (Table 3.14). In other words, high polyphenols in soil water are accompanied by low inorganic N as well as high organic N, Al^{3+} and H^+ (*cf.* Table 2.12). Together, these findings strongly suggest a mechanism similar to that proposed by *Northup et al.* [1995] for a sequence of gradually more stunted forests on increasingly acid soils in California. According to their theory, losses of precious NO_3^- in drainage water from already N-deficient sites such as the Mor-type forests are reduced by complexation of the NO_3^- ions with

polyphenols. Under such conditions concentrations of DON in soil water will be enhanced and those of NH_4^+ and NO_3^- reduced [*Northup et al.*, 1995]. As shown in Table 2.12, this is indeed the case in the Mor-type forests compared to the more N-rich Mull-type forests.

The higher concentrations of phenols in topsoil water extracted from the Mor-type forests most probably reflect exudation from fine roots rather than leaching from litter because concentrations in foliage and small roots were not much higher in the Mor-type forests (Tables 3.5 and 3.8). As such, the enhanced production of phenols by the trees in the Mor-type forests may serve the dual purpose of conserving N (by reducing leaching losses of mobile NO_3^-; *Northup et al.* [1995]) and ameliorating Al-toxicity by complexation [*Hue et al.*, 1986]. However, these distinct advantages have their ecological costs: (i) Where concentrations of phenols in litter are enhanced, they tend to retard decomposition [*Kuiters*, 1990] and (ii) It is quite possible that an increased below-ground production of secondary metabolites is achieved at the expense of above-ground forest productivity and thus stature [*Bruijnzeel and Veneklaas*, 1998]. Decomposition and mineralization of litter in the MMor forest are indeed much (s)lower than in the PMull forest (Section 9.3.1; Table 9.4). Further work is necessary to evaluate the relative importance of high Al and H, low N and the role of polyphenols in the process (*cf.* Section 10.3).

10.2 Conclusions

- There are no climatic explanations for the development of stunted forests in the Blue Mountains of Jamaica, neither in terms of excess rainfall, prolonged exposure to fog, drought, low temperatures nor low radiation hampering photosynthesis.

- With the exception of N in stunted Mor forests, intrinsically low nutrient availability is not the dominant edaphic factor determining forest physiognomy in the study area. Rather, the nutrient uptake capacity of the stunted forests seems restricted, either directly because of very high concentrations of H^+ (rendering the uptake of K more difficult) or, indirectly, via the mobilization of so much 'free' Al^{3+} that root functioning is hampered.

- Concentrations of Al^{3+} in the soil water from the Mor-type forests exceed values that are generally thought to induce conditions of chronic Al-toxicity. The resulting injury of fine roots may involve high maintenance costs, possibly at the expense of above-ground productivity.

- Mull-type and Mor-type forests seem to have developed different strategies to deal with excess Al. The trees in the Mull-type forests may dispose of excess Al by concentrating it in their foliage prior to abscission (possibly in cell walls and vacuoles, where Al does not affect cell metabolism). Mor forest trees seem unable to achieve this and instead rely on an exclusion

strategy involving below-ground exudation of secondary metabolites, including polyphenols that form strong complexes with Al and so reduce Al toxicity.

- High concentrations of Al^{3+} and phenolic compounds in soil moisture may also initiate the formation of strong complexes between Al and P or between phenols and N, thereby impairing the direct availability of P and N to plants as well.

- Also enhanced concentrations of phenols in leaf litter may retard decomposition, thus reducing nutrient availability further.

Summarizing, the present study of the hydrology and biogeochemistry of tropical montane rain forests of contrasting stature in the Blue Mountains of Jamaica illustrates that the observed contrasts in physiognomy and humus/soil morphology in the area are most probably the result of a chronically affected root system in the more stunted forest types. Both high acidity and high concentrations of 'free' Al^{3+} in the soil water of the Mor-type forests must cause direct injury to the roots, hamper nutrient uptake (notably of K) and set in motion a series of ameliorating strategies, *inter alia* the enhanced production of secondary metabolites to both complex Al and conserve nitrogen. Such adaptations come at a seemingly high ecological cost, however, in terms of retarded litter mineralization and decomposition as well as enhanced energy requirements for the production of below-ground synthates, the effect of which may be a retardation in above-ground forest productivity and thus reduced forest stature.

10.3 Recommendations for further research

In order to explain the development of forests with contrasting stature in the Blue Mountains of Jamaica more fully the following aspects merit further investigation:

- A primary gap in knowledge concerns the actual water use of the studied forests. In other words, the present, somewhat tentative, estimates of transpiration rates for the MMor and PMull forests require validation whereas additional measurements need to be made in the WMull and Mor forests. This could be achieved, for example, by (re-running) heat pulse velocity measurements with improved protection of the loggers against excess moisture or by employing isotope injection techniques [*cf. Calder*, 1992]. As useful measurements need to be obtained for contrasting forest stands on a 200–1000 m^2 scale, micro-meteorological approaches are considered less useful in this respect due to fetch limitations [*cf. Thom*, 1975]. Reliable estimates of transpiration rates for the respective forest types are of particular importance for the qualification of nutrient losses in drainage water. The latter are, in turn, essential when it comes to assessing the rates of nutrient depletion of the respective soil types [*cf.*

Bruijnzeel, 1991]. Such estimates are at present approximate (PMull and MMor forests; Chapter 7) or unknown (WMull and Mor forests).

- The quantity and quality of stemflow (and to a lesser extent throughfall) in the Mor and WMull forests of *Tanner* [1977a, 1980b] need to be examined in order to establish the water and nutrient inputs to the forest floor via net precipitation in all four forest types. As the present findings indicate an unexpectedly high contribution of stemflow and high spatial variability in both stemflow and throughfall, all future measurements should be carefully planned in terms of gauge design, network density, and sampling frequency (*cf.* Section 5.6.1).

- Although the hydrological influence of cloud water deposition (CW) in the study area has been demonstrated to be minor (Section 4.4.2), quantification of this component for the WMull and, in particular, the Mor forest would still be of interest, given the fact that nutrient inputs via CW to the MMor forest proved substantial (Section 7.4.3). Furthermore, although water inputs via fog may be small, the effects of fog-induced leaf wetness on transpiration rates are unknown. The presently used method to estimate CW inputs (*i.e.* recording throughfall during periods with zero rainfall) is unsuitable to determine to what extent canopies are wetted. Such work could employ leaf wetness sensors and should ideally be combined with the heat pulse velocity observations mentioned earlier [*cf.* *Hutley et al.*, 1997].

- Estimates of the net photosynthetic activity of the respective forests constitute another prime objective for future research. Because (i) photosynthetic capacity at the leaf level did not seem to differ between forests in the area (Section 6.3.1) and (ii) the contrasting forest types are essentially subjected to the same radiation climate (Section 4.4.3), attention should be focussed on obtaining detailed stand estimates for leaf area distribution and light attenuation throughout the canopy. Because litterfall (and thus leaf production) in the study area is seasonal (Section 8.4.1; *Tanner* [1980a]), observations of photosynthetic activity should be made throughout the year rather than on an instantaneous basis only. The combination of such measurements with the observations of water uptake listed previously would have the added advantage that the water use efficiency (*i.e.* the amount of C produced per unit of water uptake; *Landsberg* [1986]) of the respective species could be evaluated as well.

- The below-ground requirements for the production of photosynthates, *i.e.* the amounts of nutrient fluxes incorporated for the maintenance and growth of the root system, are currently unknown for all of the studied forests and indeed for all tropical montane forests. Because the present estimates of gross nutrient uptake do not include below-ground demands (only stem increment and small litter production; Tables 7.10 and 7.11), they are bound to underestimate total nutrient uptake. Furthermore, because the root biomass of the Mor and Mull-type forests are subject to

quite contrasting edaphic conditions (Tables 2.10 and 2.12) it is quite possible that the presently used relative uptake rates are as unreliable as the absolute figures. Further work is highly desirable and could follow up on the root ingrowth studies of *Stewart* [1999].

Apart from a detailed study of root dynamics (growth, mortality, decomposition) in the respective forest types, further quantitative information is required on the transfers of nutrients in, especially, the ectorganic (LFH-) horizons and (to a lesser extent) the organic (Ah-) horizon. Of special interest in this respect is the capacity of the root mats of the Mor-type forests and the root-mycorrhizal associations of the F+H horizons in the respective forest types (see Appendix A) to directly exploit nutrients in throughfall and stemflow, and in partly decomposed litter. A detailed study of the litter decomposition and water chemistry at small depth intervals within the LFH-Ah complex (*e.g.* using micro-suction samplers) might be able to shed more light on the vexed question as to whether the more stunted character of the forests on Mor humus is a cause or consequence of the development of the latter.

- It is unknown to what extent the more adverse edaphic conditions observed in the Mor topsoils (*e.g.* high acidity and Al^{3+}, low available N; Tables 2.10 and 2.12) *actually* affect forest functioning in the study area although the evidence from other sites with comparable soil characteristics would certainly suggest this. Cross-over experiments investigating the development of seedlings of key species exposed to different growth solutions (*e.g.* soil and litter extractions derived from the respective forests and/or synthesized on the basis of the presently found composition of soil moisture) may contribute significantly to the answer. The use of artificial solutions would allow the evaluation of 'threshold' values beyond which concentrations of H^+, Al^{3+} or phenolic compounds (alone or in combination) start to limit the nutrient uptake capacity of trees under the conditions encountered in the Mor-type soils. Secondly, in-situ examination of the root tips of principal tree species (rather than observed on bulk root samples) and of seedlings cultivated in solutions could help to verify to what extent the roots in the Mor-type forests actually suffer from rhizo-toxicity. Thirdly, attempts should be made to specify the Al-P, phenol-P, phenol-N, and phenol-Al complexes and their role in governing the availability of key nutrients in the soil solutions. Finally, the possibility of enhancing the nutrient uptake capacity and, consequently, tree growth in the Mor-type forests by reducing acidity and levels of Al^{3+}, should be considered, either by supplying the forest soils with NPK fertilizer in combination with liming, or by liming alone. The results of the present investigations suggest that the previous focus on fertilization with N and P only [*Tanner et al.*, 1990, 1998; *Stewart*, 1999] has been too narrow.

- Finally, the most intriguing question of all: "What is the *initial* triggering mechanism for Mor-type soil development in the Blue Mountains of

Jamaica" remains unanswered. The difference in weathering stage of the Mull and Mor-type soils, the occurrence of parent material relatively near the surface in Mor soil horizons (Appendix A), the distribution of Mor sites in relation to terrain steepness, and the high landslide potential all suggest that stunted Mor forests have developed on top of exposed subsoil material, whereas taller-statured Mull forests are situated on top of more intact residual profiles.

SAMENVATTING

De overgang tussen relatief laaggelegen maar goed ontwikkeld tropisch bergbos (lower montane forest) en hoger gelegen, veelal minder ontwikkeld bergbos (upper montane forest) wordt gekenmerkt door een aantal structurele veranderingen. Met het toenemen van de hoogte nemen de gemiddelde boomhoogte, stamdiameter en bladgrootte af terwijl het aantal stammen per oppervlakteeenheid, de dikte en stugheid van de bladeren en de hoeveelheid epifyten op stammen en takken toeneemt. Het aantal boomsoorten vermindert maar de diversiteit van soorten in de ondergroei neemt toe, evenals het aantal endemische soorten. De reductie in boomhoogte die veelal vergezeld gaat met een grillige groeiwijze van takken en stammen noemt men 'stunting'.

Op equatoriale bergen ligt, afhankelijk van de klimatologische condities, de grens tussen beide bostypen tussen de 1500 en 2500 meter. Verder van de evenaar daalt de scheidslijn waarbij opvalt dat de overgang tussen 'niet-stunted' en 'stunted' bossen op kustnabije bergen of eilanden veel lager ligt (b.v. <1000 meter) dan op meer landinwaards gelegen locaties. Er treedt als het ware compressie op van de vegetatiezones waarbij verlaging van het condensatienivo (het voorkomen van mist of bewolking op geringe hoogte) een belangrijke rol lijkt te spelen, al bestaat er tot op heden geen eenduidige verklaring voor de wijze waarop dit gebeurt. Tot de belangrijkste hypothesen omtrent het ontstaan van 'stunting' behoren o.a.:

- Reductie van inkomende straling en een dalende lucht- en bladtemperatuur door mist en lage bewolking heeft negative gevolgen voor bladfotosynthese. Verhoging van de luchtvochtigheid en verlenging van de tijd gedurende welke het kronendak nat is verlaagt de transpiratiecapaciteit van het bos, en daarmee de opname van water en nutrienten.

- Mistwater (horizontale neerslag) dat door de vegetatie wordt 'ingevangen' vormt een extra hydrologische component die samen met de verminderde transpiratie leidt tot zeer natte, anaerobe bodemcondities en een slecht functionerend wortelsysteem.

- Veelal slecht ontwikkelde bodems in mistbossen vergroten, vanwege een geringe bodemvochtcapaciteit, de kans op waterstress gedurende incidentele langdurige droogte.

- 'Stunting' is het gevolg van een beperkt nutrienten aanbod gerelateerd aan (i) intrinsiek onvruchtbare bodems; (ii) een hoge bodemzuurgraad en een beperkte opnamecapaciteit van de wortels; (iii) een lage decompositiesnelheid van organisch materiaal.

- Verhoogde concentraties secondaire metabolieten (o.a. polyfenolen) in bladmateriaal uit bossen met 'stunting' als gevolg van verschillende stressfactoren (water- en nutriententekort, blootstelling aan hoge dosis UV-B, zure bodems, aluminium-toxiciteit) hebben, direct of indirect, een negatief effect op een groot aantal ecologische processen (fotosynthese, celdeling, wortelfuncties, nutrientenbeschikbaarheid, decompositiesnelheid).

- Op onbeschutte locaties zijn hoge windsnelheden verantwoordelijk zijn voor 'stunting'.

In de regel ondervindt de vergelijking tussen 'niet-stunted' en 'stunted' bergbos hinder van het feit dat beide bostypen meestal gekenmerkt worden door een ander klimaat, een andere bodemgesteldheid en een andere soortensamenstelling. Om meer inzicht te krijgen in de processen die ten grondslag liggen aan 'stunting' is het daarom zaak het aantal variabelen terug te dringen.

Deze mogelijkheid wordt geboden in de Blue Mountains in Jamaica, waar men onder vergelijkbare geologische en klimatologische omstandigheden een serie bossen aantreft met een contrasterende structuur, bodemvorming en ecologie maar met een vergelijkbare soortensamenstelling. Structurele parameters, (bio)chemische aspecten, en bepaalde ecologische processen in deze bossen zijn uitgebreid gedocumenteerd [o.a. *Tanner*, 1977a, b, 1980b, 1985; *Tanner et al.*, 1990; *Kapos and Tanner*, 1985; *Aylett*, 1985; *Healey*, 1989]. Samen met de locale logistieke voorzieningen (Cinchona Botanical Gardens, de University of the West Indies in Kingston) maakt dit het gebied zeer geschikt voor het testen van de verschillende hypothesen omtrent het ontstaan van 'stunting'.

Om meer inzicht te krijgen in de hydrometeorologie, hydrologie, plantenfysiology en bodemchemie van bergbossen met een contrasterende boomhoogte is in 1994 onderzoek gestart in een samenwerking tussen de Vrije Universiteit Amsterdam, de Universiteit van Amsterdam en de University of Cambridge (U.K.) met financiering door de stichting voor wetenschappelijk onderzoek van de tropen (WOTRO, projectnr. W84-371) en de dr. Jacoba Ruinen stichting voor kronendak onderzoek. In november 1994 werd afgereisd naar Jamaica voor een veldwerkperiode van 19 maanden, aangevuld met een kort verblijf in februari en maart 1997.

Het onderzoek concentreert zich op de volgende vraagstellingen:

- Wat is de water- en nutrienten input via het door de vegetatie ingevangen mistwater (horizontale neerslag) en wat is de invloed van mist op het ecologisch functioneren van de betreffende bossen?

- Zijn de verschillen in bosstructuur verklaarbaar aan de hand van verschillen in de fotosynthetische capaciteit van de vegetatie?

Table A: Soortenrijkdom, boomhoogte, totaal stamoppervlak (TSO), aantal bomen per hectare, aantal bomen per hectare met meervoudige stammen (BMS) en de verhouding stammen:bomen (VSB) voor bomen met een diameter op borsthoogte ≥ 5 cm; specifiek bladoppervlak (SBO) en de bladoppervlakt index (BOI) voor het WMull, PMull, MMor en Mor bostype. Gegevens van de WMull en Mor zijn van *Tanner* [1977a, 1980b].

Bostype	Soorten per plot	Hoogte m	TSO $m^2 ha^{-1}$	Bomen ha^{-1}	BMS	VSB -	SBO $cm^2\, g^{-1}$	BOI -
WMull	34	13–17	77,9	6200	175	1,03	78	5,1
PMull	23	7–12	53,1	4400	567	1,19	60	5,0
MMor	10	5–8	44,4	6043	1043	1,29	61	4,1
Mor	16	5–7	64,7	4900	1500	1,49	60	4,1

- Is 'stunting' in de Blue Mountains een gevolg van gevoeligheid voor waterstress gedurende droogte?

- Is 'stunting' het gevolg van een beperkte nutrientenbeschikbaarheid? En zo ja, is deze gerelateerd aan decompositiesnelheid en stikstofmineralisatie, aan de activiteit van microorganismen en bodemfauna of louter het gevolg van intrinsiek nutrientarme bodems.

- Komt de mate van 'stunting' tot uiting in de chemische samenstelling van blad-, strooisel- en wortelmateriaal. En, zo ja, aan welke bodemparameters zijn deze biochemische aspecten gerelateerd.

Antwoord op deze vragen werd gezocht in een hydrologisch, hydrochemisch, en ecologisch onderzoek in vier bostypen met een contrasterende boomhoogte, bosstructuur en bodem/humus opbouw. Deze vier plots worden (met afnemende boomhoogte) aangeduid als WMull, PMull, MMor en Mor. Beide Mull bossen (boomhoogte 7–17 m) worden als 'niet-stunted' aangemerkt, beide Mor bossen (boomhoogte 5–8 m) als 'stunted'. De belangrijkste structurele verschillen tussen de vier bostypen zijn samengevat in Tabel A. De WMull en Mor zijn gelegen op *c.* 1600 m op een helling van John Crow Peak (zie figuur 2.1 op blz. 14). Beide plots zijn permanente onderzoekslocaties en, met het oog op verstoring, slechts betrokken bij de bodem-, bio-, en hydrochemische aspecten van dit onderzoek.

In de PMull en MMor werden daarentegen naast de verschillende komponenten van de waterbalans (regen, mistwater, doorval, stamafvoer, strooiselpercolaat en bodemvocht) en de nutrientenflux, ook de totale nutrienten in- en outputs, en de nutrientenflux via strooiselval gevolgd. evenals decompositie, mineralizatie, nitrificatie en activiteit van de bodemfauna. De PMull (1809 m) en MMor (1824 m) zijn gelegen op een bergrug tussen Sir John's Peak (1900 m) en Bellevue Peak (1849 m) met een onderlinge afstand van slechts 30 meter. Seizoens- en dagelijkse fluctuaties van de belangrijkste klimatologische parameters werden geregistreerd met behulp van een automatisch weerstation dat werd opgericht op Bellevue Peak.

RESULTATEN

Onderverdeling van bostypen in de Blue Mountains op basis van structuur en soortensamenstelling is goed mogelijk. In de 'stunted' Mor en MMor bossen zijn boomhoogte en soortenrijkdom beduidend lager dan in de Mull typen, stamdichtheid en de verhouding stammen:bomen zijn duidelijk hoger. Totaal boomoppervlak is slecht gerelateerd aan de mate van 'stunting'. Structurele verschillen in bladdimensies kunnen niet worden aangetoont.

De opbouw van de Mull en Mor bodems vertoont grote verschillen. De Mull bodems (geclassificeerd als Dystric cambisols) bestaan uit een dunne ($\leq$6 cm), onregelmatig ectorganische laag (strooisel, gefragmenteerd strooisel en humus) met daar onder een dikke (>3 m) kleiige minerale bodem. De worteldichtheid neemt geleidelijk af met de diepte. De Mor bodems (Folic histosols) bestaan uit een dike ($\leq$0.5 m) ectorganische laag van slecht verteerde humus en een ondiepe ($\leq$0.7 m) siltige bodem met klasten van onverweerd materiaal. Wortels zijn in dit profiel geconcentreerd boven de minerale Ah. De fysische eigenschappen van beide bodemtypen zijn zodanig dat waterverzadiging vrijwel is uitgesloten: de doorlaatbaarheid en porositeit zijn hoog (1800–10 $cm\,d^{-1}$, 80–60 %) en, belangrijker, hoger in de 'stunted' Mor dan in de Mull. Ook tijdens extreme neerslag (1500 mm gedurende 5 dagen in februari 1996) werd geen oppervlakte afvoer waargenomen. De waterhoudende capaciteit van Mor en Mull bodems vertoont geen directe relatie met de mate van 'stunting'. Echter, door de ondiepe distributie van wortels in de Mor bodems en een kleinere voor vegetatie beschikbare hoeveelheid water in de bovenste 50 cm van de bodemprofielen (130–140 mm in Mor, 170–190 mm in Mull bodems) lijkt het Mor bostype gevoeliger voor droogte dan de Mull. De diversiteit, hoeveelheid en activiteit van de bodemfauna is in de PMull aanzienlijk hoger dan in de MMor.

Hydrometeorologische aspecten
Uit dit onderzoek blijkt dat er geen klimatologische verklaring is voor het ontstaan van 'stunting' in de Blue Mountains, Jamaica. De extreem kleine laterale afstand tussen verschillende bostypen (30 m) sluit een louter meteorologische verklaring uit. Neerslag over 1995 bedroeg 3060 mm; de gemiddelde jaarlijkse neerslag wordt geschat op 2850 mm. Regenbuien zijn van relatief korte duur en de intensiviteit is laag. Neerslag valt verspreid over het jaar, oktober en november zijn relatief nat (>350 mm), maart en juli relatief droog (<90 mm). De input van mistwater in het PMull en MMor bos wordt geschat op slechts 1.4 en 3.4 % van de jaarlijkse neerslag en is te gering om de structurele verschillen tussen de bossen te verklaren. Over 1995 bedroeg de totale hoeveelheid inkomende straling op Bellevue peak (1849 m) 5040 $MJ\,m^{-2}$; de reductie door bewolking wordt geschat op 47 %. Gedurende 80 % van de relevante uren lag de intensiteit van de straling boven de drempelwaarde voor lichtverzadigde fotosynthese. Algemeen gesteld is de gemiddeld intensiteit van 13.8 $MJ\,m^{-2}$ per dag ruim voldoende voor de ontwikkeling van 'niet-stunted' bergbos. De luchttemperatuur boven de vegetatie bedraagt overdag gemiddeld 17 ^{o}C; tijdens zware bewolking gemiddeld 16 ^{o}C. Onderzoek door *Kapos and*

Tanner [1985] heeft uitgewezen dat lucht- en bladtemperatuur in het gebied niet noemenswaardig van elkaar verschillen. Lage lucht- en bladtemperatuur zijn daarom geen verklaring voor 'stunting' in de Blue Mountains. De gemiddelde windsnelheid was laag (4.1 $m\,s^{-1}$ op 1849 m). Er zijn geen aanwijzingen dat cyclonen (die Jamaica gemiddelt eens per 15 jaar passeren) meer schade aanrichten aan 'stunted' Mor dan aan 'niet-stunted' Mull bos.

De netto neerslag (de som van doorval en stamafvoer) bedroeg 86 % van de regenval in de PMull en 78 % in de MMor. De interceptie verliezen waren respectievelijk 14 en 22 %. In zowel de PMull als MMor was de stamafvoer buitengewoon hoog (13 en 18 % van de neerslag). Watergebruik (verdamping) werd bepaald met behulp van de Penman-Monteith vergelijking. De verdamping over 1995 wordt geschat op 509 *mm* (17 % van de neerslag) voor de vegetatie op Bellevue Peak en de 'stunted' MMor en op 620 *mm* (20 % van de neerslag) voor de PMull. Deze waarden zijn niet laag en zijn vergelijkbaar met schattingen voor bergbossen die slechts in beperkte mate blootstaan aan mist. Gezien de lage input van mistwater en de relatief hoge jaarlijkse verdamping speelt mist geen grote rol bij de ontwikkeling van 'stunting' in de Blue Mountains.

Drainage in de PMull over 1995 werd geschat op 2032 *mm*, die in de MMor op 1857 *mm*. Uit simulaties met behulp van een ééndimensionaal transportmodel blijkt dat de eerste tekenen van bodemvochtstress (vochtspanning <-100 *kPa*) zich in de MMor en PMull bodemprofielen kunnen voordoen na droge perioden van respectievelijk 14 of 40 dagen. Pas na een droge periode van respectievelijk 6–12 weken (MMor) of 18 weken (PMull) zou permamente schade (verwelking) kunnen optreden (vochtspanning <-1.58 *MPa*). Gezien het regenvalpatroon in de Blue Mountains is het optreden van dergelijk lange droge perioden hoogst onwaarschijnlijk.

Fotosynthese

In het huidige onderzoek bleek het logistiek niet haalbaar metingen aan fotosynthese uit te voeren onder actuele licht condities. Metingen werden beperkt tot bepalingen van maximale fotosynthese (als maat voor de fotosynthetische capaciteit) onder artificieel licht. Maximale fotosynthese tussen de boomsoorten loopt sterk uiteen, maar verschillen tussen bostypen binnen één en dezelfde soort kunnen niet worden aangetoon. Stikstofconcentraties en isotopensamenstelling (δ^{13} C) van bladmateriaal, specifieke bladmassa's en de dichtheid en grootte van stomata vertonen het zelfde patroon. Geen van deze parameters vertoont een trend met de mate van 'stunting'. Het is daardoor niet aannemelijk dat de fotosynthetische capaciteit op bladnivo tussen de verschillende bostypen veel verschilt. Een eventueel lagere productiviteit in de Mor bossen is daarom waarschijnlijk slechts gerelateerd aan de hoeveel bladoppervlak en kronendakstructuur, factoren die eerder een gevolg van 'stunting' zijn dan een oorzaak.

Bodemchemische aspecten

De resultaten van dit onderzoek laten slechts een beperkte relatie zien tussen de mate van 'stunting' in een bepaald bostype en de hoeveelheid beschikbare nutrienten. Individuele concentraties van $BaCl_2$-uitwisselbare elementen in de

bodem vertonen geen duidelijk trend met 'stunting' al vertoont de som van de uitwisselbare kationen een daling met afnemende boomhoogte. Ondanks het feit dat concentraties van de meeste elementen (waaronder nitraat, ammonium, fosfaat en kalium) in strooiselpercolaat afnemen met een toenemende mate van 'stunting' (WMull>PMull>MMor>Mor) bestaat deze trend niet voor de overige kationen, totaal stikstof and fosfaat in water uit de top van de minerale bodem (waar zich de meerderheid van de wortels bevindt). De concentraties kationen, totaal stikstof, fosfaat en totaal fosfor in bodemvocht uit het meest 'stunted' bostype (de Mor) zijn slechts weining lager of zelfs hoger (voor totaal fosfor) dan die uit het meest ontwikkelde bos, de WMull. Daarnaast blijkt dat de concentraties in het strooiselpercolaat en die in het bodemvocht niet noemenswaardig lager zijn dan die in goed ontwikkelde (>30 m) bergbossen elders.

Concentraties H^+ in het bodemvocht uit de toplagen van de 'stunted' Mor bossen zijn hoger dan die in het bodemvocht uit de Mull bossen evenals de concentraties 'vrij' aluminium Al^{3+} (1.1–1.5 $\mu mol\, l^{-1}$ in Mull, 15–20 $\mu mol\, l^{-1}$ in Mor bos). De molaire verhouding calcium:aluminium in bodemvocht neemt drastisch af met een toenemende mate van 'stunting'.

Samengevat lijkt het erop dat niet de hoeveel nutrienten in de bodem bepalend is voor de mate van 'stunting' in de Blue Mountains maar dat de beschikbaarheid van deze elementen de belangrijkste rol speelt. De nutrientenopname, en met name die van kalium, in de Mor bossen wordt daarbij vooral gehinderd door de hoge concentratie H^+ of door hoge concentratie Al^{3+} die in het Mor bodemwater dermate hoog is dat er sprake zou kunnen zijn van chronische aluminium-toxiciteit en schade aan het wortelstelsel. Een hoge concentratie Al^{3+} verhindert de opname van kationen, leidt tot vorming van aluminium-fosfor complexen (die de beschikbaarheid van fosfor verminderen) en een verhoogde productie secondaire metabolieten (o.a. polyfenolen) in wortels induceren. Polyfenolen vormen niet alleen complexe verbindingen met Al^{3+} (en verminderen hierdoor de toxiciteit) maar ook met het zeer mobiele nitraat (wat mogelijk de uitspoeling van nitraat voorkomt maar ook de beschikbaarheid voor planten vermindert).

Uit dit onderzoek blijkt dat zowel concentraties van Al^{3+}, polyphenolen, organisch gebonden aluminium, organisch-stikstof (DON) en organisch-fosfor (DOP) hoger zijn in het Mor/MMor bodemvocht dan in het bodemvocht uit WMull/PMull. De concentraties nitraat, de netto productie van nitraat en de netto stikstof mineralisatie zijn hoger in PMull dan in MMor.

Chemische aspecten van plantenmateriaal

Uit het onderzoek naar de chemie van blad-, strooisel- en wortelmateriaal en de chemie van strooiselpercolaat en bodemvocht blijkt dat 'stunting' in de Blue Mountains geen duidelijke invloed heeft op de chemie van plantenmateriaal. Desondanks blijkt dat de concentraties aluminium in bladeren uit de WMull/PMull hoger (0.07–0.19 $mg\, g^{-1}$) zijn dan in materiaal uit de Mor/MMor (0.05–0.13 $mg\, g^{-1}$), ondanks het feit dat de concentraties H^+ en Al^{3+} in bodemvocht veel hoger zijn in de Mor bodems. Gaande van Mull naar Mor bos neemt de verhouding calcium:aluminium in het bladmateriaal (en in de wortels)

toe terwijl deze in het bodemvocht sterk afneemt. Dit contrast neemt toe met de leeftijd van de bladeren en is het sterkst in bladstrooisel: aluminium concentraties in PMull bladstrooisel zijn 3 tot 4 keer die in de MMor. In geen van de plots kunnen de onderzochte boomsoorten worden aangeduid als aluminium-accumulator. De concentraties fosfor in bladmateriaal zijn laag in zowel de Mull als Mor bossen maar vertonen geen trend met 'stunting': de laagste concentraties fosfor worden gevonden in de bladeren uit het meest ontwikkeld bos (de WMull). De concentratie kalium in bladeren neemt wel af met toenemende mate van 'stunting' wat zou kunnen wijzen op een opnamebeperking van dit element. In de wortels nemen de concentraties kalium, aluminium en totaal stikstof af naarmate 'stunting' toeneemt maar calcium, magnesium, fosfor, en polyphenolen vertonen geen trend. Een directe relatie tussen bodemzuurgraad en concentraties polyfenolen in bladmateriaal zoals gevonden door *Northup et al.* [1995] kan niet worden aangetoond.

De relatief hoge concentraties aluminium in wortels en strooisel uit de goed ontwikkelde WMull en PMull wijzen mogelijk op een accumulatiestrategie waarbij aluminium gecomplexeerd wordt in celwanden en vacuoles (waar het geen toxische werking heeft). Het lijkt er op dat de bomen in de Mor en MMor hier niet toe in staat zijn. Zij verminderen de toxiciteit van aluminium door middel van ondergrondse uitscheiding van secondaire metabolieten (o.a. polyfenolen), die complexe (niet schadelijke) verbindingen aangaan met aluminium. De kosten van de aanmaak van deze metabolieten zijn echter hoog [*Whipps and Lynch*, 1986] wat kan leiden tot een verminderde bovengrondse productiviteit.

Nutrientenflux

De nutrienten input via neerslag in de PMull is gelijk aan die in de MMor. In de PMull bedraagt de input via mistwater tussen 3 % (kalium en ammonium) en 14 % (magnesium, nitraat) van de input via neerslag, in de MMor tussen 7 en 35 %. De totale nutrienten input via netto neerslag (doorval plus stamafvoer) in de MMor was 25–30 % lager (kalium, natrium, chloor, ammonium) of gelijk (calcium, magnesium, fosfaat, nitraat) aan dat in de PMull. De nutrientenflux via strooiselpercolaat (nutrienten die gemakkelijk door de vegetatie kunnen worden opgenomen) in de MMor was 45–75 % lager dan die in de PMull. Voor zowel de PMull als de MMor blijkt de jaarlijkse input van nutrienten via regen en mist (veel) groter te zijn dan de jaarlijkse netto opname (de hoeveelheid nutrienten die jaarlijk wordt vastgelegd in stamgroei). Naast de totale hoeveelheid nutrienten in de bodem houdt dus ook de jaarlijkse input geen verband met de mate van 'stunting' in de Blue Mountains. Netto nutrienten verlies (input via regen minus verlies via drainage) was gemiddeld lager in de MMor plot. De nutrienten input via strooiselpercolaat is zowel in de PMull als in de MMor groter dan de totale opname (geschat aan de hand van jaarlijkse strooiselval en stamgroei) met uitzondering van stikstof en fosfor. De verschillen in nutrientendynamiek tussen beide plots zijn gering en kunnen het optreden van 'stunting' in de Mor plots niet verklaren.

Ondanks de verschillen in boomhoogte en structuur tussen de PMull en

MMor zijn de verschillen in strooiselval klein (6.5 $kg\,ha^{-1}\,yr^{-1}$ in de PMull, 6.2 $kg\,ha^{-1}\,yr^{-1}$ in de MMor). De hoeveelheden strooisel op de bosbodem in de MMor is daarentegen aanzienlijk groter dan die in de PMull (11.0 en 7.5 $t\,ha^{-1}$). Dit geeft aan dat de decompositiesnelheid van organisch materiaal in het 'stunted' MMor bos lager ligt dan die in de PMull. Een decompositie experiment met strooiselzakjes bevestigt deze veronderstelling.

De totale hoeveelheid nutrienten die de bosbodem bereikt via netto neerslag (doorval en stamafvoer), strooiselval, en mineralisatie (in geval van stikstof) is toereikend voor de geschatte totale nutrienten opname in de beide bossen, met uitzondering van een tekort aan stikstof (12 %) in de MMor. Echter, indien men de rekening houdt met decompositiesnelheid van het strooisel in respectievelijk de PMull en MMor ontstaat een stikstof tekort van 20 % in de PMull en een algemeen nutrienten tekort in de MMor (o.a. 29 % voor fosfor, 75 % voor stikstof). Het grote verschil in beschikbaarheid aan stikstof is mogelijk het meest directe bewijs voor een stikstoftekort in de 'stunted' bossen in de Blue Mountains.

CONCLUSIES

Op grond van het onderzoek '*Hydrologie en biogeochemie van tropische montane regenwouden met contrasterende boomhoogte in the Blue Mountains, Jamaica*' kom ik met betrekking tot het optreden van 'stunting' tot de volgende conclusies:

- Er is geen klimatologische verklaring, in termen van overvloedige regenval, extra input van mistwater, lagere lucht- en bladtemperaturen of gereduceerde stralingsinput, voor het voorkomen van 'stunting' in bergbossen in de Blue Mountains.

- Er zijn met uitzondering van stikstof geen aanwijzingen voor een intrinsiek hoger nutriententekort in Mor bodems ten opzichte van Mull bodems. Er zijn echter aanwijzingen dat de opnamecapaciteit van wortels in de Mor bodem sterk wordt belemmerd door hoge concentraties H^+ (die de opname van met name kalium beperken), of indirect, via de mobilisatie van 'vrij' aluminium (Al^{3+}).

- Concentraties van Al^{3+} in het bodemwater in de Mor en MMor zijn dermate hoog dat er waarschijnlijk sprake is van aluminium-toxiciteit. Aantasting van het wortelstelsel, hoge 'onderhoudskosten' en een beperking van de nutrientenopname zijn hiervan het gevolg.

- Mull en Mor bossen lijken verschillende strategieën te hanteren met betrekking tot aluminium. Bomen in Mull bossen concentreren en immobiliseren aluminium in de bladeren. Bomen in Mor bossen lijken hiertoe niet in staat en verminderen de opname van Al^{3+} door middel van productie en uitscheiding van sterk aluminium-complexerende verbindingen (o.a. polyfenolen).

- Naast aantasting van het wortelstelsel leidt een hoge concentratie Al^{3+} tot een verminderde beschikbaarheid aan fosfor door de vorming van aluminium-fosfor complexen. Verhoogde concentraties fenolen daarentegen verlagen mogelijk de directe beschikbaarheid van stikstof door de vorming van complexen met nitraat maar verhinderen tevens uitspoeling van het mobile nitraat.

- De verhoogde concentraties fenolen in bladmateriaal uit de Mor bossen vertragen de decompositiesnelheid. Dit resulteert in een verdere afname van de beschikbare hoeveelheid nutrienten.

Samenvattend: deze studie naar de hydrologie en biogeochemie van bergbossen met een contrasterende boomhoogte in de Blue Mountains in Jamaica illustreert dat het contrast in bosstructuur en humus/bodem morfologie in dit gebied waarschijnlijk het gevolg is van een chronische aantasting van het wortelstelsel in de 'stunted' Mor bossen. Zowel de hoge zuurgraad als de hoge concentraties Al^{3+} in het bodemwater van de Mor bossen brengen mogelijk directe schade toe aan de wortels, bemoeilijken de opname van nutrienten (met name kalium) en induceren een reeks strategieën ter vermindering van de aluminiumtoxiciteit, waaronder een verhoogde productie van secondaire metabolieten die leiden tot aluminium-complexering en vermindering van de uitspoeling van stikstof. De ecologische kosten van deze aanpassingen zijn echter hoog, door de vertraging van decompositie- en mineralisatiesnelheden in strooisel en door de hoge ondergrondse productiekosten van deze verbindingen. Het effect hiervan is een verlaging van de bovengrondse productiviteit en een reductie in boomhoogte.

ACKNOWLEDGEMENTS

This thesis reflects the efforts of a large number of people who have participated in this study or who have supported me otherwise throughout the field work in Jamaica, the analyses of data, or the writing phase of this thesis. Without their help it would not have been possible to finish this project successfully.

The research was financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO), under grant no. W76–371 and through a bequest by the late Mrs. Dr Jacoba Ruinen which is gratefully acknowledged. Equipment, materials, facilities and logistics were provided by the Faculty of Earth Sciences of the Vrije Universiteit Amsterdam. In addition, I am grateful to the Forest Department of the Government of Jamaica for the permission to work in the Blue Mountain National Park; to the successive Heads of the Department of Botany (now Department of Life Sciences) from the University of the West Indies (Dr Devi Prasad, Dr Ph. Coates-Beckford and Dr Steele) for allowing me to use their office- and lab facilities; and to the Director of Public Gardens in Jamaica for letting me use Cinchona Botanical Gardens as a permanent field station.

At the time, my copromotor Sampurno Bruijnzeel, lured me into the field of environmental hydrology and montane cloud forest ecology using a fine selection of slides and promises of sandy beaches on tropical islands. It proved to be good tactics, for to me they were an irresistible bait. Now, almost ten years later, I have to admit that reality lived up to the expectations that emerged from his slide shows. Over the years he has become a mentor, and very pleasant companion at the office or on numerous occasions outside the university. I want to thank him dearly for his unconditional support, for the continued discussions and critical remarks during every phase of the project, and especially for his great efforts to improve earlier drafts of this thesis. Sampurno, terima kasih banyak!

I am grateful to Dr Herman Verhoef. As my second copromotor, I like to thank him for his time and enthusiasm while introducing me to the world of soil ecology and for his critical remarks on the pertinent sections of this thesis. Without his influence this study would have been less comprehensive.

I am particularly indebted to Dr Edmund Tanner who introduced me to the research area and whose previous work in Jamaica proved essential within the context of this study. I thank him for his guidance in the field, for his help

during the inventory of the forest plots, for his thorough and critical comments on this dissertation, and for his hospitality during my stay in Panama in 1999. Asking him for help or advice never proved to be in vain! Likewise, I gratefully acknowledge the Conville & Caius College of the University of Cambridge for allowing me to make use of their ADC–LCA2 equipment as well as the College Land Rover. As transportation was essential during the studies, me, my guests, the students and the supervisors all benefited from this generosity.

I like to thank Prof. Dr Hans Vugts for reviewing this thesis and for his willingness to the help me out whenever I was struggling with technical or scientific problems in the field of meteorology. Over the years I have borrowed excessively from his collection of meteorological instruments (for a fair price, of course!) but I am particularly thankful for the replacements that he provided after meteorological instruments in Jamaica had been destroyed by lightning.

Prof. Dr J. M. Verstraten, Department of Physical Geography, University of Amsterdam, is thanked for his advice on soil chemistry, arranging the analyses of DOC of water samples and for reviewing this thesis. Prof. Dr N. M. van Straalen, Faculty of Biology, Vrije Universiteit Amsterdam, is also gratefully acknowledged for reviewing this dissertation. I express my thanks to Prof. Dr Ian Simmers for being my promotor, for his support during the studies and for arranging the necessary paper work that inevitably emerges during the final stage of a Ph.D.

It has been a pleasure to work with Dr Erik Veneklaas whose help was crucial during the field measurements of photosynthesis and for the analysis of isotopes in foliar material. I appreciate his enthusiasm and time spent on critically reviewing drafts of Chapter 6 of this dissertation. The International Centre for Agriculture in the Tropics (CIAT) in Cali, Colombia (where Dr Veneklaas was appointed in 1995) is acknowledged for the use of their lab facilities. I also like to thank Dr Niek Jan Bink for his thorough comments on all micro-meteorological sections in this dissertation; Rene Hogervorst for his work on soil fauna analyses and his help during the preparation of Chapter 9, Rik Zoomer for his time spent on the soil ecological analyses, and Dr Jelte Rozema for his comments on the photosynthetic section (Chapter 6).

The work by Tini Bäer, John Kist, Hetty Schäfer, Martin Konert and Roel van Elzas from the Water and Soil Laboratories of the FES–VUA to analyse the extensive sets of water and soil samples is gratefully acknowledged. Many thanks for the all the help and advice! Piet Wartenberg of the water lab of the Department of Physical Geography, University of Amsterdam, is thanked for his analysis of the dissolved organic carbon and nitrogen species and Dr Tom Nielsen (Kopenhavs Universitet) for the analysis of the gas samples. Dr Tom Goodland (University of Wales) is thanked for his work on the enumeration of the forest understorey.

I like to thank Michel Groen, Theo Hamer, Nico van Harlingen, Hans Bakker, Jan Vink, Johan de Lange and Ron Lootens from the FES-VUA Equipment Department, the Mechanical Workshop and the Department of Electronics for their technical support and education during my studies at the VUA. Over the years their patience has been tested on many occasions but they were always ready to

help me materialize another crazy idea. Without their help and enthusiasm 'kippertjes', wheeled kitchen stoves, and vintage British motorcycles would never have left the drawing board or storage boxes. Many thanks!

Without Dr Morag McDonald my stay in Jamaica would not have been the same; it was a pleasure having her as a colleague working at Cinchona. I want to thank her dearly for her help in getting settled in Jamaica, for her company, her hospitality and her willingness to share her office with a guy like me. I thank her for introducing me to diving, to the Carib Theatre, and to Gloria's Restaurant. Morag, hugs and kisses!

During my stay in Jamaica I frequently enjoyed the hospitality of Dr Devi Prasad (Department of Botany, University of the West Indies) and his family who allowed me to use his laboratory and invited me to stay at their residence whenever necessary. I also like to thank Thera Edwards for all her help, advice and hospitality during my residence in Jamaica and Ir Marc van der Herten and Mr Neville for teaching me the arts of motorcycle riding & maintenance. Nothing better than the Junction Road at sunrise!

Mr. Lloyd Stamp and his co-workers (Steve, Brian, Albert, Perry and Mr Edwards) of the Cinchona Botanical Garden are gratefully acknowledged for their hospitality during my stay at the field station. I am grateful to them for their help in the field, their work during my absence in December 1995, the continuous supply of fresh vegetables, the nightly entertainment, their attempts to teach me Jamaican country-style cooking and their efforts to get the Land Rover on four wheels again after an accident early in the fieldwork phase. Respect, men! Respect!

The former MSc. students Roland Bronckers, Agnes Chardonnens, Dennis Elbers, Sander van Hesteren, Richard de Jeu, Sandra Saras, Lilian Spijkerman, and Menco Wierda all came to Jamaica to assist me with field measurements or participated in the numerous analytical procedures in Amsterdam. It is thanks to them that it was possible to collect the wide variety and amount of data on which this dissertation is based. Forget about the rain, the mist, the cold and the smell of damp sleeping bags. Remember the bright Cinchona nights, Appelton Special, cheap movies in crazy theaters, hot Blue Mountain coffee, and Red Stripe beer. Remember Lime Cay, Frenchman's Cove, Treasure Bay, and San San beach, or the ackee & saltfish, curried coat, sweet & sour chicken, dumplins and the patties, rice & pies, and Guinea pig. It may never come back, it will never be the same.

I want to thank all participants of the daily 'koffie tafel' and brothers-in-arms Arnoud, Ben, Jaap, Joost, Michiel and Paul for the many 'after-work' activities and support during the last couple of years. Without them life would have been a lot less fun! Congratulations and success to all of you! I particularly like to thank Jaap Schellekens, my room mate, who found the patience to share an office with me for over 3 years. His help, advice and comments on data processing, programming and writing this dissertation proved invaluable!

I like thank Ineke and Louis for all their support, love, and consideration from 1968 onwards. And, finally, I thank Jet for never, not ever, losing faith.

REFERENCES

Adams, C. D., *Flowering plants of Jamaica*, University of the West Indies, Mona, Kingston, Jamaica, 1972.

Amacher, M. C., R. E. Henderson, M. D. Breithhaupt, C. L. Seale, and J. M. LaBauve, Unbuffered and buffered salt methods for exchangeable cations and effective cation-exchange capacity, *Soil Science Society of America Journal*, *54*, 1036–1042, 1990.

Anderson, D. W., The effect of parent material and soil development on nutrient cycling in temperate ecosystems, *Biogeochemistry*, *5*, 71–97, 1988.

Anderson, J. M., and M. J. Swift, Decomposition in tropical rain forests, in *The tropical rainforest*, edited by S. L. Sutton, A. C. Chadwick, and T. C. Whitmore, pp. 287–309, Blackwell Scientific Publications, Oxford, U. K., 1983.

Anderson, J. M., J. Proctor, and H. W. Vallack, Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter, *Journal of Ecology*, *71*, 503–527, 1983.

Appelo, C. A. J., and D. Postma, *Geochemistry, groundwater and pollution*, A. A. Balkema, Rotterdam. The Netherlands, 1993.

Asbury, A. E., W. H. McDowell, R. Trinidad–Pizarro, and S. Berrios, Solute deposition from cloud water to the canopy of a Puerto Rican montane forest, *Atmospheric Environment*, *28*, 1773–1780, 1994.

Ash, J., Stunted cloud forest in Taveuni, Fiji, *Pacific Science*, *41*, 191–199, 1987.

Aylett, G. P., Irradiance interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees, *Photosynthetica*, *19*, 323–337, 1985.

Bartlett, R. J., and D. C. Riego, Effect of chelation on the toxicity of aluminium, *Plant and Soil*, *37*, 419–423, 1972.

Baynton, H. W., The ecology of an elfin forest in Puerto Rico, 2: The microclimate of Pico del Oeste, *Journal of the Arnold Arboretum*, *49*, 419–430, 1968.

Baynton, H. W., The ecology of an elfin forest in Puerto Rico, 3: Hilltop and forest influences on the microclimate of Pico del Oeste, *Journal of the Arnold Arboretum*, *50*, 80–92, 1969.

Bellingham, P. J., *The effects of a hurricane on Jamaican montane rain forest*, Ph.D. thesis, Cambridge University, Cambridge, U. K., 1993.

Belmans, C., J. G. Wesseling, and R. A. Feddes, Simulation model of the water balance of a cropped soil: SWATRE, *Journal of Hydrology*, *63*, 271–286, 1983.

Berg, B., and H. Staaf, Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition, *Ecological Bulletin*, *32*, 373–390, 1980.

Berg, B., and H. Staaf, Leaching, accumulation and release of nitrogen in decomposing forest litter, *Ecological Bulletin*, *33*, 163–178, 1981.

Berg, M. P., *Decomposition, nutrient flow and food web dynamics in a stratified pine forest soil*, Ph.D. thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1997.

Berg, M. P., J. P. Kniese, R. Zoomer, and H. A. Verhoef, Long-term decomposition of successive organic strata in a nitrogen saturated Scots pine soil, *Forest Ecology and Management*, *107*, 159–172, 1998.

Beven, K., and P. Germann, Macropores and water flow in soils, *Water Resources Research*, *18*, 1311–1325, 1982.

Black, C. A., D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clark, Automated ascorbic acid reduction method, in *Methods of Soil Analyses Part 2: Chemical and Microbiological Properties*, pp. 1043–1044, American Society of Agronomy, Madison, Wisconsin, U. S., 1965.

Bolt, G. H., *Basic elements*, vol. A of *Soil chemistry*, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands, 1976.

Box, J. D., Investigation of the Folin-Ciocalteau reagent for the determination of polyphenolic substances in natural waters, *Water Research*, *17*, 511–525, 1983.

Bridgman, H. A., J. L. Walmsley, and R. S. Schemenauer, Modelling the spatial variations of wind speed and direction on Roundtop Mountain, Quebec, *Atmospher-Ocean*, *32*, 605–619, 1994.

Bronckers, R. H. E., and S. van Hesteren, *An introductory comparison of two forest ecosystems in the tropical montane rain forests of the Blue Mountains of Jamaica*, Msc. thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1995.

Brouwer, L. C., *Nutrient cycling in pristine and logged forest in tropical rain forest. A study in Guyana*, Ph.D. thesis, Universiteit Utrecht, Utrecht, The Netherlands, 1996.

Brown, M. B., I. de la Roca, A. Vallejo, G. Ford, J. Casey, B. Aguilar, and R. Haacker, A valuation analysis of the role of cloud forests in watershed protection. Sierra de las Minas Biosphere Reserve, Guatamala and Cusuco National Park, Honduras, *project report*, RARE Center for Tropical Conservation, U. S., 1996.

Brown, W. H., *Vegetation of Philippine mountains, the relation between the environment and physical types at different altitude*, Bureau of Science, Manila, 1919.

Bruijnzeel, L. A., M. J. Waterloo, J. Proctor, A. T. Kuiters, and B. Kotterink, Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the '*Massenerhebung*' effect, *Journal of Ecology*, *81*, 145–167, 1993.

Bruijnzeel, L. A., Elemental concentration of litterfall in a lower montane rain forest in Central Java, Indonesia, *Malayan Nature Journal*, *37*, 199–208, 1984.

Bruijnzeel, L. A., Nutrient content of bulk precipitation in South-central Java, Indonesia, *Journal of Tropical Ecology*, *5*, 187–202, 1989a.

Bruijnzeel, L. A., Nutrient cycling in moist tropical forests: the hydrological framework, in *Mineral nutrients in tropical forest and savanna ecosystems*, edited by J. Proctor, pp. 383–415, Blackwell Scientific Press, Oxford, 1989b.

Bruijnzeel, L. A., *Hydrology of moist tropical forests and effects of conversion: a state of knowledge review*, Unesco International Hydrological Programme, Paris, France, 1990.

Bruijnzeel, L. A., Nutrient input – output budgets for tropical forest ecosystems: a review, *Journal of Tropical Ecology*, *7*, 1–24, 1991.

Bruijnzeel, L. A., Hydrology of tropical montane cloud forests: a reassessment, in *Paper presented at the Second International Colloquium on hydrology and water management in the humid tropics, Panama City, 1999*, UNESCI-IHP, 1999.

Bruijnzeel, L. A., and J. Proctor, Hydrology and biogeochemistry of tropical montane cloud forest: what do we really know?, in *Tropical montane cloud forests*, edited by L. S. Hamilton, J. O. Juvik, and F. N. Scatena, vol. 110 of *Ecological Studies*, pp. 38–78, Springer Verlag, New York, 1995.

Bruijnzeel, L. A., and E. J. Veneklaas, Climatological conditions and tropical montane forest productivity: the fog has not lifted yet, *Ecology*, *79*, 3–9, 1998.

Bruijnzeel, L. A., and H. A. Verhoef, Forest stunting on wet tropical mountains, with special reference to the Blue Mountains, Jamaica, *Research proposal file no. W84-371*, The Netherlans Foundation for the Advancement of Tropical Research WOTRO, The Hague, the Netherlands, 1994.

Brünig, *Ecological studies in the Kerangas Forest of Sarawak and Brunei*, Borneo Literature Bureau of the Sarawak Forest Department, Kuching, Malaysia, 1970.

Brutsaert, W. H., *Evaporation into the atmosphere*, D. Reidel Publishing Company, Dordrecht, The Netherlands, 1982.

Burghouts, T., *Spatial heterogeneity of nutrient cycling in Bornean rain forest*, Ph.D. thesis, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands, 1993.

Burghouts, T. B. A., N. M. van Straalen, and L. A. Bruijnzeel, Spatial heterogeneity of element and litter turnover in a Bornean rain forest, *Journal of Tropical Ecology*, *14*, 477–506, 1998.

Bush, M. B., Some effects of physical processes on the redevelopment of the forests of krakatau, *Tech. rep.*, University of Hull, Department of Geography, Hull, UK, 1986.

Cahn, M. D., D. R. Bouldin, and M. S. Cravo, Amelioration of subsoil acidity in an Oxisol of the humid tropics, *Biology and Fertility of Soils*, *15*, 153–159, 1993.

Calder, I. R., Deuterium tracing for the estimation of transpiration from trees. Part2. Estimation of transpiration rates and transpiration parameters using a time-averaged deuterium tracing method, *Journal of Hydrology*, *130*, 27–35, 1992.

Cavelier, J., *The ecology of elfin cloud forests in northern South America*, Dissertation submitted for the annual research fellowship competition, Trinity College, University of Cambridge, Cambridge, U. K., 1988.

Cavelier, J., *Root biomass, production and the effect of fertilization in two tropical rain forests*, Ph.D. thesis, University of Cambridge, Cambridge, U. K., 1989.

Cavelier, J., Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains, in *Tropical forest plant ecophysiology*, edited by S. Mulkey, R. L. Chazdon, and A. P. Smith, pp. 399–439, Chapman & Hall, New York, 1996.

Cavelier, J., and G. Goldstein, Mist and fog interception in elfin cloud forests in Colombia and Venezuela, *Journal of Tropical Ecology*, *5*, 309–322, 1989.

Cavelier, J., and C. Mejia, Climatic factors and tree stature in the elfin cloud forest of Serrania de Macuira, Colombia, *Agricultural and Forest Meteorology*, *53*, 105–123, 1990.

Cavelier, J., and M. C. Peñuela, Soil respiration in the cloud forest and dry deciduous forest of Serrania de Macuira, Colombia, *Biotropica*, *22*, 346–352, 1990.

Cavelier, J., D. Solis, and M. A. Jaramillo, Fog interception in the montane forests across the Central Cordillera of Panama, *Journal of Tropical Ecology*, *12*, 357–369, 1996.

Cavelier, J., M. A. Jaramillo, D. Solis, and D. de León, Water balance and nutrient inputs in bulk precipitation in tropical montane cloud forest in Panama, *Journal of Hydrology*, *193*, 83–96, 1997.

Chandler, G., Mineralization and nitrification in three Malaysian forest soils, *Soil Biology and Biochemistry*, *17*, 347–353, 1985.

Chardonnens, A., Leaf thickness and UV-B absorbing pigments of trees and herbs in relation to stunted tropical mountain forest growth and to an elevational gradient along the Blue Mountains, Jamaica, *internal report*, Vrije Universiteit, Amsterdam, The Netherlands, 1996.

Chazdon, R. L., Light variation and carbon gain in rain forest understorey palms, *Journal of Ecology*, *74*, 995–1012, 1986.

Cheng Yang, J., and H. Insam, Microbial biomass and relative contribution of bacteria and fungi in soil beneath tropical rain forest, Hainan Island, China, *Journal of Tropical Ecology*, *7*, 385–393, 1991.

Cintron, G., Variation in size and frequency of stomata with altitude in the Luquillo Mountains, in *A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico*, edited by H. Odum and R. Pidgeon, pp. H133–H135, U.S. Atomic Energy Commission, Oak Ridge, Tennessee, U. S., 1970.

Clark, K. L., N. M. Nadkarni, D. Schaeffer, and H. L. Gholz, Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica, *Journal of Tropical Ecology*, *14*, 27–45, 1998.

Coleman, D. C., and D. A. Crossley, *Fundamentals of soil ecology*, Academic Press, San Diego, California, U. S. A., 1996.

Comstock, J., and J. Ehleringer, Stomatal response to humidity in common beans (*Phaseolus vulgaris*): implications for maximum transpiration rate, water-use efficiency and productivity, *Australian Journal of Plant Physiology*, *20*, 669–691, 1993.

Cooper, J. D., Water use of a tea estate from soil moisture measurements, *East African Agricultural and Forestry Journal, Special issue*, pp. 102–121, 1979.

Cornejo, F. H., A. Varela, and S. J. Wright, Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria, *Oikos*, *70*, 183–190, 1994.

Coulson, C. B., R. I. Davies, and D. A. Lewis, Polyphenols of leaves, litter and superficial humus from mull and mor sites, *Journal of Soil Science*, *11*, 20–29, 1960.

Cronan, C. S., and D. F. Grigal, Use of calcium/aluminum ratios as indicators of stress in forest ecosystems, *Journal of Environmental Quality*, *24*, 209–226, 1995.

Cuenca, G., R. Herrera, and E. Medina, Aluminium tolerance in trees of a tropical cloud forest, *Plant and Soil*, *125*, 169–175, 1990.

Cuevas, E., and E. Medina, Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization, *Oecologia*, *68*, 466–472, 1986.

Cuevas, E., and E. Medina, Nutrient dynamics within Amazonian forest ecosystems. II. Fine root growth nutrient availability and leaf litter decomposition, *Oecologia*, *76*, 222–235, 1988.

Culf, A. D., G. Fish, and M. G. Hodnett, The albedo of Amazonian forest and ranchland, *Journal of Climate*, *8*, 1544–1554, 1995.

Dalling, J. W., *Regeneration on landslides in the Blue Mountains, Jamaica*, Ph.D. thesis, University of Cambridge, Cambridge, U. K., 1992.

Davidson, E. A., P. A. Matson, P. M. Vitousek, R. Riley, K. Dunkin, G. Garcia-Méndez, and J. M. Maass, Processes regulating soil emissions of NO and N_2O in a seasonally dry tropical forest, *Ecology*, *74*, 130–139, 1993.

Davies, R. I., Relation of polyphenols to decomposition of organic matter and to pedogenetic processes, *Soil Science*, *111*, 80–85, 1971.

Davis, S. H., R. A. Vertessy, D. L. Dunkerley, and R. G. Main, The influence of scale on the measurement of saturated conductivity in a forest soil, in *23rd Hydrology and Water Resources Symposium*, pp. 103–108, Hobart Australia, 1996.

De Bruin, H. A. R., *The energy balance of the earth's surface: a practical approach*, Ph.D. thesis, Wageningen Agricultural University, Wageningen, The Netherlands, 1982.

Dohrenwend, R. E., Hydrologic behavior at the top of a tropical mountain, *Research Note 29*, Michigan Technological University, Michigan, 1979.

Doumenge, C., D. Gilmour, M. R. Perez, and J. Blockhus, Tropical montane cloud forests: conservation status and management issues, in *Tropical montane cloud forests*, edited by L. S. Hamilton, J. O. Juvik, and F. N. Scatena, vol. 110 of *Ecological Studies*, pp. 24–37, Springer Verlag, New York, 1995.

Drechsel, P., and W. Zech, Foliar nutrient levels in broad-leaved tropical trees: A tabular overview, *Plant and Soil*, *131*, 29–46, 1991.

Driscoll, C. T., and W. D. Schecher, Aluminium in the environment, in *Aluminium and its role in biology*, edited by H. Sigel and A. Sigel, vol. 24 of *Metal ions in biological systems*, pp. 59–122, Marcel Dekker Inc., New York, U. S., 1988.

Ducatti, C., E. Salati, and D. Martins, Measurements of the natural variation of $^{13}C/^{12}C$ ratio in leaves at Reserve Ducke Forest, central Amazonia, *Forest Ecology and Management*, *38*, 201–210, 1991.

Duchaufour, P., *Pédologie. I. Pédogenèse et Classification*, Masson, Paris, France, 1983.

Dye, P. J., B. W. Olbrich, and I. R. Calder, A comparison of the heat pulse method and deuterium tracing methods for measuring transpiration from *Eucalyptus grandis* trees, *Journal of Experimental Botany*, *43*, 337–343, 1992.

Edwards, P. J., Studies of mineral cycling in a montane rain forest in New Guinea. II. The production and disappearance of litter, *Journal of Ecology*, *65*, 971–992, 1977.

Edwards, P. J., Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall, *Journal of Ecology*, *70*, 807–827, 1982.

Edwards, P. J., and P. J. Grubb, Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil characteristics and the division of mineral elements between the vegetation and soil, *Journal of Ecology*, *70*, 649–666, 1982.

Ehleringer, J. R., Stable isotopes, in *Plant physiological ecology: field methods and instrumentation*, edited by R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, Chapman and Hall, New York, 1989.

Ehleringer, J. R., Carbon and water relations in desert plants: an isotopic perspective, in *Stable isotopes and plant carbon-water relations*, edited by J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, pp. 155–172, Academic Press, San Diego, 1993.

Ehleringer, J. R., and T. A. Cooper, Correlations between carbon isotope ratio and microhabitat in desert plants, *Oecologia*, *76*, 562–566, 1988.

Ehleringer, J. R., A. E. Hall, and G. D. Farquhar, *Stable isotopes and plant carbon/water relations*, Academic Press, San Diego, 1993.

Einhellig, F. A., and L. Y. Kuan, Effects of scopoletin and chlorogenic acid on stomatal aperture in tobacco and sun flower, *Bulletin of the Torrey Botanical Club*, *98*, 155–162, 1971.

Einhellig, F. A., E. L. Rice, P. G. Risser, and S. H. Wender, Effects of scopoletin on growth, CO_2 exchange rates, and concentration of scopoletin, scopolin, and chlorogenic acids, *Bulletin of the Torrey Botanical Club*, *97*, 22–33, 1970.

Elbers, D., *Microbial activity and biomass in relation to litter decomposition in two forest ecosystems in the Blue Mountains of Jamaica*, Msc. thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1996.

Eriksson, E., The yearly circulation of chlorine and sulphur in nature, *Tellus*, *12*, 63–109, 1960.

Ewel, J. J., Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala, *Journal of Ecology*, *64*, 293–309, 1976.

Faber, J. H., A. Teuben, M. P. Berg, and P. Doelman, Microbial biomass and activity in pine litter in the presence of *Tomocerus minor* (Insecta, Collembola), *Biology and Fertility of Soils*, *12*, 233–240, 1992.

FAO-UNESCO, *Soil Map of the World. With revised legend*, International Soil Reference and Information Centre (ISRIC), Wageningen, The Netherlands, 1990.

Farquhar, G. D., M. H. O'Leary, and J. A. Berry, On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Australian Journal of Plant Physiology*, *9*, 121–137, 1982.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick, Carbon isotope discrimination and photosynthesis, *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*, 503–537, 1989.

Feddes, R. A., P. J. Kowalik, and H. Zarasny, *Simulation of field water use and crop yield*, John Wiley & Sons, 1978.

Field, C. B., On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants, *Australian Journal of Plant Physiology*, *15*, 343–358, 1988.

Firestone, M. K., and E. A. Davidson, Microbiological basis of NO and N_2O production and consumption in soil, in *Exchanges of trace gasses between terrestrial ecosystems and the atmosphere*, edited by M. O. Andreae and D. S. Schimmel, John Wiley & Sons, London, U. K., 1989.

Fischer, J., and L. L. Tieszen, Carbon isotope characterization of vegetation and soil organic matter in subtropical forests in Luquillo, Puerto Rico, *Biotropica*, *27*, 138–148, 1995.

Foy, C. D., R. L. Chaney, and M. C. White, The physiology of metal toxicity in plants, *Annual Review of Plant Physiology*, *29*, 511–566, 1978.

Frahm, J. P., and S. R. Gradstein, An altitudinal zonation of tropical rain forests using byrophytes, *Journal of Biogeography*, *18*, 669–676, 1991.

Gash, J. H. C., An analytical model of rainfall interception by forests, *Quarterly Journal of the Royal Meteorological Society*, *105*, 43–55, 1979.

Gash, J. H. C., and A. J. Morton, An application of the Rutter model to the estimation of the interception loss from Thetford Forest, *Journal of Hydrology*, *38*, 49–58, 1978.

Gash, J. H. C., C. R. Lloyd, and G. Lachaud, Estimating sparse forest rainfall interception with an analytical model, *Journal of Hydrology*, *170*, 79–86, 1995.

Gates, D. M., The ecology of an elfin forest in Puerto Rico. 4. Transpiration rates and temperatures of leaves in cool humid environments, *Journal of the Arnold Arboretum*, *50*, 93–98, 1969.

Gautam-Basak, M., and J. Proctor, Micronutrients, aluminium, silicon and ash in leaf litterfall from forests in Gunung Mulu National Park, Sarawak, *Malaysian Forester*, *46*, 224–232, 1983.

Gentry, A. G., and C. H. Dobson, Diversity and biogeography of neotropical vascular epiphytes, *Annals of the Missouri Botanical Garden*, *74*, 205–233, 1987.

Gershenzon, J., Changes in levels of plant secondary metabolites under water and nutrient stress, *Recent Advances in Phytochemistry*, *18*, 273–320, 1984.

Gill, A. M., The ecology of an elfin forest in Puerto Rico. 6. Aerial roots, *Journal of the Arnold Arboretum*, *50*, 197–209, 1969.

Glass, A. D. M., Influence of phenolic acids on ion uptake. I. Inhibition of phosphate uptake, *Plant Physiology*, *51*, 1037–1041, 1973.

Glass, A. D. M., Influence of phenolic acids on ion uptake. III. Inhibition of potassium absorption, *Journal of Experimental Botany*, *25*, 1104–1113, 1974.

Gordon, C. A., R. Herrera, and T. C. Hutchinson, Studies of fog events at two cloud forests near Caracas, Venezuela - II. Chemistry of fog, *Atmospheric Environment*, *28*, 323–337, 1994.

Grieve, I. C., J. Proctor, and S. A. Cousins, Soil variation with altitude on Volcan Barva, Costa Rica, *Catena*, *17*, 525–534, 1990.

Grubb, P. J., Factors controlling the distribution of forest types on tropical mountains: new facts and a new perspective, in *Altitudinal zonation in Malesia, transaction of the third Aberdeen symposium on Malesian ecology*, edited by J. R. Flenley, pp. 13–46, University of Hull, Hull, U. K., 1974.

Grubb, P. J., Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition, *Annual Review of Ecology and Systematics*, *8*, 83–107, 1977.

Grubb, P. J., The role of mineral nutrients in the tropics: a plant ecologist's view, in *Mineral nutrients in tropical forest and savanna ecosystems*, edited by J. Proctor, pp. 417–439, Blackwell Scientific Press, Oxford, 1989.

Grubb, P. J., and E. V. J. Tanner, The montane forests and soils of Jamaica: a re-assessment, *Journal of the Arnold Arboretum*, *57*, 313–368, 1976.

Grubb, P. J., and T. C. Whitmore, A comparison of montane and lowland rainforest in Ecuador. II. The climate and its effect on the distribution and physiognomy of forests, *Journal of Ecology*, *54*, 303–333, 1966.

Grubb, P. J., J. R. Lloyd, T. D. Pennington, and T. C. Whitmore, A comparison of montane and lowland rain forest in Ecuador. I. the forest structure, physiognomy and floristics, *Journal of Ecology*, *51*, 567–601, 1963.

Grubb, P. J., E. A. A. Grubb, and I. Miyata, Leaf structure and function in evergreen trees and shrubs of Japanese warm temperate rain forest. i. The structure of the lamina., *Botanical Magazine, Tokyo 88*, 197–211, 1975.

Gunadi, B., *Decomposition and nutrient flow in a pine forest plantation in Central Java*, Ph.D. thesis, Vrije Universiteit Amsterdam, Amsterdam, 1993.

Hafkenscheid, R. L. L. J., *Hydrological observations in rain forests of contrasting stature on Gunung Rakata (Krakatau), Indonesia, with special reference to the 'Massenerhebung' effect*, Msc. thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1994.

Hafkenscheid, R. L. L. J., L. A. Bruijnzeel, and R. A. M. de Jeu, Estimates of fog interception by montane rain forest in the Blue Mountains of Jamaica, in *First International Conference on Fog and Fog Collection*, edited by R. S. Schemenauer and H. Bridgman, pp. 33–36, Vancouver, 1998.

Hafkenscheid, R. L. L. J., L. A. Bruijnzeel, R. A. M. de Jeu, and N. J. Bink, Water budgets of two upper montane rain forests of contrasting stature in the Blue Mountains, Jamaica, in *Proceedings of the Second International Colloguium on Hydrology and Water Management in the Humid Tropics*, vol. (In press), Cathalac, 1999.

Hamilton, L. S., J. O. Juvik, and F. N. Scatena, *Tropical montane cloud forests*, vol. 110 of *Ecological Studies*, Springer-Verlag, New York, U. S., 1995.

Hansen, E. A., and A. R. Harris, Validity of soil-water samples collected with porous ceramic cups, *Soil Science Society of America Journal*, *39*, 528–536, 1975.

Harr, R. D., Fog drip in the Bull Run municipal watershed, Oregon, *Water Resources Bulletin*, *18*, 785–789, 1982.

Haynes, R. J., and R. S. Swift, The effects of pH and air-drying on absorption of phosphate by aluminum-organic matter associations, *Journal of Soil Science*, *40*, 773–781, 1989.

Healey, J. R., A bioassay study of soils in the Blue Mountains of Jamaica, in *Mineral nutrients in tropical forest and savanna ecosystems*, edited by J. Proctor, pp. 273–288, Blackwell Scientific Press, 1989.

Healey, J. R., *Regeneration in a Jamaican montane tropical rainforest*, Ph.D. thesis, Cambridge University, Cambridge, U. K., 1990.

Heaney, A., and J. Proctor, Chemical elements in litter in forests on Volcán Barva, Costa Rica, in *Mineral nutrients in tropical forest and savanna ecosystems*, edited by J. Proctor, pp. 255–271, Blackwell Scientific Publications, U. K., 1989.

Hendershot, W. H., and M. Duquette, A simple barium chloride method for determining cation exchange capacity and exchangeable cations, *Soil Science Society of America Journal*, *50*, 605–608, 1986.

Henderson, A., S. P. Churchill, and J. L. Luteyn, Neotropical plant diversity, *Nature*, *351*, 21–22, 1991.

Hendrix, P. F., *Earthworm ecology and biogeography in North America*, Lewis, Boca Raton, Florida, 1995.

Herrera, R., *Nutrient distribution and cycling in an Amazon Catingaa forest on Spodosols in southern Venezuela*, Ph.D. thesis, University of Reading, Reading, UK, 1979.

Herrmann, R., Die Zeitliche Anderung der Wasserbindung im Boden unter verschiedenen Vegetationsformationen der Höhenstufen eines tropischen Hochgebirges (Sierra Nevada de Santa Marta, Kolumbien), *Erdkunde*, *25*, 90–102, 1971.

Hetsch, W., and H. Hoheisel, Standorts- und Vegetations-gliederung in einem tropischen Nebelwald, *Allgemeine Forst- und Jagd Zeitung*, *147*, 200–209, 1976.

Hogan, K. P., Photosynthesis in two neotropical palm species, *Functional Ecology*, *2*, 371–377, 1988.

Hogan, K. P., A. P. Smith, and M. Samaniego, Gas exchange in six tropical semi-deciduous forest canopy tree species during the wet and dry seasons, *Biotropica*, *27*, 324–333, 1995.

Hogervorst, R. F., H. R. Zoomer, and H. A. Verhoef, Decomposition and microflora changes in spruce-forested catchments at Gårdsjön following reduced acidic deposition, in *Experimental reversal of acid rain effects: The Gårdsjön roof project*, edited by H. Hultberg and R. Skeffington, pp. 293–306, John Wiley & Sons, Sussex, U. K., 1997.

Holwerda, F., *A study of evaporation from lowland and montane tropical rain forest in the Luquillo Mountains, Puerto Rico*, Master's thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1997.

Horner, J. D., J. R. Gosz, and R. G. Cates, The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems, *American Naturalist*, *132*, 869–883, 1988.

Howard, R. A., The ecology of an elfin forest in Puerto Rico. 1. Itroduction and composition species, *Journal of the Arnold Arboretum*, *49*, 381–418, 1968.

Hue, N. V., G. R. Craddock, and F. Adama, Effects of organic acids on aluminum toxicity of subsoils, *Soil Science Society of America Journal*, *50*, 28–34, 1986.

Hunt, G. A., and R. Fogel, Fungal hyphal dynamics in a western Oregon Douglas-fir stand, *Soil Biology and Biochemistry*, *15*, 641–649, 1983.

Hunt, H. W., D. C. Coleman, E. R. Ingham, R. E. Ingham, E. T. Elliot, J. C. Moore, S. L. Rose, C. P. P. Reid, and C. R. Morley, The detrital food web in a shortgrass prairie, *Biology and Fertility of Soils*, *3*, 57–68, 1987.

Hutley, L. B., D. Doley, D. J. Yates, and A. Boonsaner, Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog, *Australian Journal of Botany*, *45*, 311–329, 1997.

Ishibashi, M., and I. Terashima, Effects of continuous leaf wetness on photosynthesis: adverse aspects of rainfall, *Plant, Cell and Environment*, *18*, 431–438, 1995.

Jackson, I. J., Relationships between rainfall parameters and interception by tropical rainforest, *Journal of Hydrology*, *24*, 215–238, 1975.

Jaffe, M. J., Morphogenetic responses of plants to mechanical stimuli or stress, *BioScience*, *30*, 239–243, 1980.

Jane, G. T., and T. G. Green, Patterns of stomatal conductance in six evergreen tree species from a New Zealand cloud forest, *Biotropical Gazet*, *146*, 413–420, 1985.

Janzen, D. H., Tropical blackwater rivers, animals, and mast fruiting by the dipterocarpaceae, *Biotropica*, *6*, 69–103, 1974.

Janzen, D. H., The insects: introduction, in *Costa Rican natural history*, edited by D. H. Janzen, pp. 619–645, The University of Chicago Press, Chicago, U. S., 1983.

Jarvis, P. G., and J. W. Leverenz, Productivity of temperate, deciduous and evergreen forests, in *Ecosystem processes: mineral cycling, productivity and man's influence*, edited by O. L. Land, P. S. Nibel, C. D. Osmond, and H. Ziegler, vol. 12D of *Physiological plant ecology: new series*, pp. 233–280, Springer-Verlag, New York, U. S. A., 1983.

Jordan, C. F., Stemflow and nutrient transfer in a tropical rain forest, *Oikos*, *31*, 257–263, 1978.

Jordan, C. F., *An Amazonian rain forest*, vol. 2 of *Man and the biosphere series*, Parthenon Publishing, Carnford, U. K. , 1989.

Jordan, C. F., and J. Heuveldop, The water budget of an Amazonian rainforest, *Acta Amazonica*, *11*, 87–92, 1981.

Jordan, C. F., R. L. Todd, and G. Escalante, Nitrogen conservation in a tropical rain forest, *Oecologia*, *39*, 123–128, 1979.

Juvik, J. O., and D. Nullet, Comments on 'A proposed standard fog collector for use in high-elevation regions', *Journal of Applied Meteorology*, *34*, 2108–2110, 1995.

Kapos, V., *An ecological investigation of sclerophylly in two tropical forests*, Ph.D. thesis, Washington University, Washington, U. S., 1982.

Kapos, V., and E. V. J. Tanner, Water relations of Jamaican upper montane rain forest trees, *Ecology*, *66*, 241–250, 1985.

Keeney, D. R., Prediction of soil nitrogen availability in forest ecosystems: a literature review, *Forest Science*, *25*, 159–171, 1980.

Keeney, D. R., Nitrogen – Inorganic forms, in *Methods of soil analysis. Part 2. Chemical and microbiological properties*, pp. 643–698, American Society of Agronomy, Madison, Wisconsin, U. S. A., 1982.

Keller, M., T. J. Gorneau, S. C. Wofsy, W. A. Kaplan, and M. B. McElroy, Production of nitrous oxide and consumption of methane by forest soils, *Geophysical Research Letter*, *10*, 1156–1159, 1983.

Kelliher, F. M., R. Leuning, M. R. Raupach, and E. D. Schulze, Maximum conductance for evaporation from global vegetation types, *Agricultural and Forest Meteorology*, *73*, 1–16, 1995.

Kessler, J., and R. J. Oosterbaan, Determining hydraulic conductivity of soils, in *I.L.R.I. Publication no. 16. Volume III.*, pp. 253–296, International Institute for Land Reclamation and Improvement, Wageningen, The Netherlands, 1973.

Khanna, P. H., and B. Ulrich, Soil characteristics influencing nutrient supply in forest soils, in *Nutrition of forest trees in plantations*, pp. 79–117, Academic Press, London, U. K., 1984.

Kimmins, J. P., Some statistical aspects of sampling throughfall precipitation in nutrient cycling studies in British Colombian coastal forests, *Ecology*, pp. 1008–1019, 1973.

Kinraide, T. B., Identification of the rhizotoxic aluminium species, *Plant and Soil*, *134*, 167–178, 1991.

Kinraide, T. B., and D. R. Parker, Apparent phytotoxicity of mononuclear hydroxy-aluminum to four dicotyledonous species, *Physiol. Plant.*, *17*, 283–288, 1990.

Kira, T., Community architecture and organic matter dynamics in tropical lowland rain forests of South-east Asia with special reference to Pasoh Forest, West Malaysia, in *Organic matter dynamics*, edited by Tomlinson and Zimmerman, pp. 561–590, 1978.

Kitayama, K., Biophysical conditions of the montane cloud forests of Mount Kinabalu, Sabah, Malaysia, in *Tropical montane cloud forests*, edited by L. S. Hamilton, J. O. Juvik, and F. N. Scatena, vol. 110 of *Ecological Studies*, pp. 183–197, Springer-Verlag, New York, U. S., 1995.

Kitayama, K., H. Taitio, D. Mueller-Dombois, and E. A. G. Schuur, Wood volume, foliar chemical composition, and soil nitrogen turn over of *Metrosideros polymorpha* (Myrthaceae) stands on a slope of Mount Haleakala, Hawaii, *Biotropica*, *30*, 330–338, 1998.

Kjøller, A., and S. Struwe, Microfungi in ecosystems: fungal occurrence and activity in litter and soil, *Oikos*, *39*, 391–422, 1982.

Kobza, J., and F. A. Einhellig, The effects of ferulic acid on mineral nutrition of grain sorgum, *Plant and Soil*, *98*, 99–109, 1987.

Kochian, L. V., Cellular mechanisms of aluminium toxicity and resistance in plants, *Annual Review of Plant Physiology and Plant Molecular Biology*, *46*, 237–260, 1995.

Konert, M., and J. Vandenberghe, Comparison of laser grain size analysis with pipette and sieve analysis: a solution for the underestimation of the clay fraction, *Sedimentology*, *44*, 523–535, 1997.

Körner, C., Leaf diffusive conductance in the major vegetation types of the globe, in *Ecophysiology of photosynthesis*, edited by E. D. Schultze and M. M. Caldwell, vol. 100 of *Ecological Studies*, pp. 462–490, Springer, Heidelberg, 1994.

Körner, C., A. Allison, and H. Hilscher, Altitudinal variation of leaf conductance and leaf anatomy in heliophytes of montane New Guinea and their interrelation with microclimate, *Flora*, *174*, 91–135, 1983.

Körner, C., G. D. Farquhar, and Z. Roksandic, A global survey of carbon isotope discrimination in plants from high altitude, *Oecologia*, *74*, 623–632, 1988.

Körner, C., G. D. Farquhar, and S. C. Wong, Carbon isotope discrimination by plants follows latitudinal and altitudinal trends, *Oecologia*, *88*, 30–40, 1991.

Kuiters, A. T., Role of phenolic substances from decomposing forest litter in plant-soil interactions, *Acta Botanica Neerlandica*, *39*, 329–348, 1990.

Kuiters, A. T., and H. M. Sarink, Effects of phenolic acids on growth, mineral composition and chlorophyll content of several deciduous and coniferous trees, *Zeitschrift fur Pflanzenernahrung and Bodenkunde*, *150*, 94–98, 1987.

Kunkel, I., and P. Kunkel, Litter fall in a Guatemalan primary forest, with details of leaf-shredding by common three species, *Journal of Ecology*, *67*, 665–686, 1979.

Kursar, T. A., Evaluation of soil respiration and soil co_2 concentrations in a lowland moist forest in Panama, *Plant and Soil*, *113*, 21–29, 1989.

Lamprecht, H., Der Gebirgs-Nebelwald der Venezolanischen Anden, *Schweizerische Zeitschrift für Forstwesen*, *2*, 1–26, 1958.

Landon, J. R., *Booker tropical soil manual: a handbook for soil survey and agricultural land evaluation in the tropics and subtropics*, Longman Scientific & Technical, Harlow, U. K., 1991.

Landsberg, J. J., *Physiological ecology of forest productivity*, Academic Press, London, 1986.

Lang, A. R. G., Simplified estimate of leaf area index from transmittance of the sun's beam, *Agricultural and Forest Meteorology*, *41*, 179–186, 1987.

Lauer, W., Die Vegetationszonierung der Neotropis and ihr Wandel seit der Eiszeit, *Ber. dt. bot. Ges.*, *99*, 211–235, 1986.

Lawton, R. O., Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation, *Australian Journal of Botany*, *69*, 1224–1230, 1982.

Lee, K. E., *Earthworms: their ecology and relationships with soils and land use*, Academic Press, Sydney, Australia, 1985.

Lee, R., Theoretical estimates versus forest water yield, *Water Resources Research*, *6*, 1327–1334, 1970.

Leigh, E. G., Structure and climate in tropical rain forest, *Annual Review of Ecology and Systematics*, *6*, 67–86, 1975.

Levitt, J., *Water, radiation, salt and other stresses*, vol. 2 of *Responses of plants to environmental stresses*, Academic Press, New York, U. S., 1980.

Liebermann, D., M. Lieberman, R. Peralta, and G. S. Hartshorn, Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica, *Journal of Ecology*, *84*, 137–152, 1996.

Lloyd, C. R., and A. Marques-Filho, Spatial variability of throughfall and stemflow measurements in Amazonian rain forest, *Agricultural and Forest Meteorology*, *42*, 63–73, 1988.

Loveless, A. R., A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves, *Annual Botany*, *25*, 168–184, 1961.

Lowry, J. B., D. W. Lee, and B. Stone, Effects of drought on Mount Kinabalu, *Malayan Nature Journal*, *26*, 178–179, 1973.

Lüttge, U., *Physiological ecology of tropical plants*, Springer-Verlag, Berlin, Germany, 1997.

Lyford, W. H., The ecology of an elfin forest in Puerto Rico. 7. Soil, root, and earthworm relationships, *Journal of the Arnold Arboretum*, *50*, 210–224, 1969.

Maggs, J., and B. Hewett, Soil and litter respiration in rainforest of contrasting and physiognomic structure near Lake Eacham, northeast Queensland, *Australian Journal of Ecology*, *15*, 329–336, 1990.

Malmer, A., *Dynamics of Hydrology and Nutrient Losses as Response to Establishment of Forest Plantation: A Case Study on Tropical Rainforest Land in Sabah, Malaysia*, Ph.D. thesis, Swedish University of Agricultural Sciences, Faculty of Forestry, S-901 83 Umeå, Sweden, 1993.

Mamanteo, B. P., and V. P. Veracion, Measurements of fogdrip, throughfall and stemflow in the mossy and Benguet pine (*Pinus kesiya*, Royle ex Gordon) forests in the upper Agno river basin, *Sylvatrop (Philippines Forest Research Journal)*, *10*, 271–282, 1985.

Marquardt, D. W., An algorithm for least-square estimates of nonlinear parameters., *Journal of the Society of Industrial Applications of Mathematics*, *11*, 431–441, 1963.

Marrs, R. H., J. Proctor, A. Heaney, and M. D. Mountford, Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica, *Journal of Ecology*, *76*, 466–482, 1988.

Marschner, H., Mechanisms of adaption of plants to acid soils, *Plant and Soil*, *134*, 1–20, 1991.

Matson, P. A., and P. M. Vitousek, Cross-system comparisons of soil nitrogen transformations and nitrous oxide flux in tropical forest ecosystems, *Global Biochemical Cycles*, *1*, 163–170, 1987.

McDonald, M., Nutrient cycling in secondary forests in the Blue Mountians of Jamaica, *In prep. for Forest Ecology and Management*, *000*, 000–000, 2000.

McKinnon, K., G. Hatta, and H. H. . A. Mangalik, *Mountain habitats*, chap. 7, pp. 315–352, Periplus Editions, Hongkong, 1996.

Medina, E., and H. Klinge, Productivity of tropical forests and tropical woodlands, in *Encylopedia of plant physiology (new series)*, vol. 12D of *Physiological plant ecology IV*, pp. 281–303, Springer-Verlag, Berlin, 1983.

Medina, E., and P. Minchin, Stratification of $\delta^{13}C$ values of leaves in Amazonian rain forests, *Oecologia*, *45*, 377–378, 1980.

Medina, E., M. Sobrado, and R. Herrera, Significance of leaf orientation for leaf temperature in an Amazonian sclerophyll vegetation, *Radiation and Environmental Biophysics*, *15*, 131–140, 1978.

Medina, E., E. Cuevas, and P. L. Weaver, Composición foliar y transpiración de especies leñosas de Pico de Este, Sierra de Luquillo, Puerto Rico, *Acta Cient. Venez.*, *32*, 159–165, 1981.

Medina, E., L. Sternberg, and E. Cuevas, Vertical stratification of $\delta^{13}C$ values in closed natural and plantation forest in the Luquillo mountains, Puerto Rico, *Oecologia*, *87*, 369–372, 1991.

Meinzer, F. C., P. W. Rundel, G. Goldstein, and M. R. Sharifi, Carbon isotope composition in relation to leaf gas exchange and environmental conditions in Hawaiian *Methrosideros polymorpha* populations, *Oecologia*, *91*, 305–311, 1992.

Mohr, E. C. J., F. A. van Baren, and J. van Schuylenborgh, *Tropical soils*, Mouton-Ichtiar Baru-Van Hoeven, The Hague, The Netherlands, 1972.

Moloney, K. A., L. J. Stratton, and R. M. Klein, Effects on simulated acidic, metal containing precipitation on coniferous litter decomposition, *Canadian Journal of Botany*, *61*, 3337–3342, 1983.

Monteith, J. L., Evaporation and the environment, in *Symposium of the Society of Experimental Biology no. 19*, pp. 245–269, 1965.

Monteith, J. L., and M. H. Unsworth, *Principles of environmental physics*, 2nd ed., Chapman and Hall, New York, 1990.

Mulkey, S. S., K. Kitajima, and S. J. Wright, Plant physiological ecology of tropical forest canopies, *Tree*, *11*, 408–412, 1996.

Muller, R. N., P. J. Kalisz, and T. W. Kimmerer, Intraspecific variation in production of astringent phenolics over a vegetation-resource availability gradient, *Oecologia*, *72*, 211–215, 1987.

Nadkarni, N. M., and T. J. Matelson, Biomass and nutrient dynamics of epiphytic litterfall in a neotropical montane forest, Costa Rica, *Biotropica*, *24*, 24–30, 1992a.

Nadkarni, N. M., and T. J. Matelson, Biomass and nutrient dynamics of fine litter of terrestrial rooted material in a neotropical montane forest, Costa Rica, *Biotropica*, *24*, 113–120, 1992b.

National Meteorological Service of Jamaica, An overview of the climate of Jamaica, *Technical report*, National Meteorological Service of Jamaica, Kingston, Jamaica, 1986.

Natrella, M. G., Experimental statistics, *Technical report*, National Bureau of Standards, Washington, 1963.

Neitske, M., *Der Einfluß von Aluminium auf die Keimung und Keimlingsbildung der Buche (Fagus silvatica, L.) unter Berucksichtigung von Wechselwirkungen mit Calcium und Stickstofform*, Ph.D. thesis, Wilhelms-Universität Münster, Münster, Germany, 1984.

Nicolai, V., Phenolic and mineral content of leaves influences decomposition in European forest communities, *Ecology*, *75*, 575–579, 1988.

Nortcliff, S., and J. B. Thornes, Variations in soil nutrients in relation to soil moisture status in a tropical forested ecosystem, in *Mineral Nutrient in Tropical Forest and Savanna Ecosystems*, edited by J. Proctor, pp. 137–151, Blackwell Scientific Publications, London, U. K., 1989.

Northup, R., R. A. Dahlgren, and Z. Yu, Intraspecific variation of conifer phenolic concentration on a marine terrace soil acidity gradient: a new interpretation, *Plant and Soil*, *171*, 255–262, 1995.

Odum, H. T., Rain forest structure and mineral cycling homeostasis, in *A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico*, edited by H. T. Odum and R. F. Pidgeon, pp. H3–H52, U.S. Atomic Energy Commission, Oak Ridge, Tennessee, 1970.

Oguntoyinbo, J. S., Reflection coefficient of natural vegetation, crops and urban surfaces in Nigeria, *Quarterly Journal of the Royal Meteorological Society*, *96*, 430–441, 1970.

Ohsawa, M., The montane cloud forest and its gradational zonation in southern and eastern Asia, in *Tropical montane cloud forests*, edited by L. S. Hamilton, J. O. Juvik, and F. N. Scatena, vol. 110 of *Ecological Studies*, pp. 254–265, Springer-Verlag, New York, U. S., 1995.

Oke, T. R., *Boundary layer climates*, 2nd ed., Methuen, London, 1987.

Oliver, B. G., E. M. Thurman, and R. L. Malcolm, The contribution of humic substances to the acidity of colored natural waters, *Geochimica et Cosmochimica Acta*, *47*, 2031–2035, 1983.

Olson, D. M., The distribution of leaf litter invertebrates along a neotropical altitudinal gradient, *Journal of Tropical Ecology*, *10*, 129–150, 1994.

Olson, J. S., Energy storage and the balance of producers and decomposers in ecological systems, *Ecology*, *44*, 322–331, 1963.

Ovington, J. D., and J. S. Olson, Biomass and chemical content of El Verde lower montane rain forest plants, in *A tropical rain forest*, edited by H. T. Odum and R. F. Pidgeon, pp. H53–H77, U.S. Atomic Energy Commission, Oak Ridge, Tennessee, 1970.

Parker, G. G., Throughfall and stemflow in the forest nutrient cycle, *Advances in Ecological Research*, *13*, 57–133, 1983.

Parker, G. G., *The effect of disturbance on water and solute budgets of hillslope tropical rainforest in northeastern Costa Rica*, Ph.D. thesis, University of Georgia, Athens, Georgia, U. S., 1985.

Parkhurst, D. L., User's guide to PHREEQC - a computer program for speciation, reaction-path, advective-transport, and inverse geochemical calculations, *Water-Resources Investigations Report 95–4227*, U.S. Geological Survey, 1995.

Patterson, D. T., Effects of allelopathic chemicals on growth and physiological responses of soybean (*Glycine max*), *Weed Science*, *29*, 53–59, 1981.

Pearcy, R. W., Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understorey micro-enviroments, *Functional Ecology*, *1*, 169–178, 1987.

Pearcy, R. W., and H. W. Calkin, Carbon dioxide exchange of ^{3}C and ^{4}C tree species in the understorey of a Hawaiian forest, *Oecologia*, *58*, 26–32, 1983.

Pearcy, R. W., J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, *Plant physiological ecology: field methods and instrumentation*, Chapman and Hall, New York, 1989.

Pendry, C. A., and J. Proctor, The causes of altitudinal zonation of rain forests on Bukit Belalong, Brunei, *Journal of Ecology*, *84*, 407–418, 1996a.

Pendry, C. A., and J. Proctor, Preliminary studies of altitudinal zonation and nitrogen supply on Bukit Belalong, Brunei, in *Tropical rainforest research - current issues*, edited by D. S. Edwards, W. E. Booth, and S. C. Choy, pp. 241–257, Kluwer Academic Publishers, The Netherlands, 1996b.

Penman, H. L., Evaporation: An introductory survey, *Netherlands Journal of Agricultural Sciences*, *4*, 9–29, 1956.

Persson, R., *World forest resources*, Royal College of Forestry, Stockholm, Sweden, 1974.

Pierce, L. L., and S. W. Running, Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer, *Ecology*, *69*, 1762–1767, 1988.

Pinker, R. T., O. E. Thompson, and T. F. Eck, The albedo of a tropical evergreen forest, *Quarterly Journal of the Royal Meteorological Society*, *106*, 551–558, 1980.

Powers, R. F., Mineralizable soil nitrogen as an index of nitrogen availability to forest trees, *Soil Science Society of America Journal*, *44*, 1314–1320, 1980.

Proctor, J., Tropical forest litterfall. I. Problems of data comparison, *Special Publication of The Britisch Ecological Society*, pp. 267–273, 1983.

Proctor, J., Tropical forest litterfall. II. The data set, in *Tropical rain-forest: the Leeds Symposium*, edited by A. C. Chadwick and S. L. Sutton, pp. 83–113, Leeds Philosophical and Literary Society, Leeds, UK, 1984.

Proctor, J., Nutrient cycling in primary and old secondary rainforests, *Applied Geography*, *7*, 135–152, 1987.

Proctor, J., J. M. Anderson, S. Fogden, and H. W. Vallack, Ecological studies in four contrasting lowland rainforest in Gunung Mulu National Park, Sarawak: II. Litterfall, litter standing crop and preliminary observations on herbivory, *Journal of Ecology*, *71*, 261–283, 1983a.

Proctor, J., J. M. Anderson, and H. W. Vallack, Comparative studies on forests, soils and litterfall at four altitudes on Gunung Mulu, Sarawak, *The Malaysian Forester*, *46*, 60–75, 1983b.

Proctor, J., Y. F. Lee, A. M. Langley, W. R. C. Munro, and T. Nelson, Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia I. Environment, forest structure and floristics, *Journal of Ecology*, *76*, 320–340, 1988.

Proctor, J., C. Phillips, G. K. Duff, A. Heaney, and F. M. Robertson, Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. II. Some forest processes, *Journal of Ecology*, *77*, 317–331, 1989.

Proctor, J., A. J. M. Baker, M. M. J. van Balgooy, L. A. Bruijnzeel, S. H. Jones, and D. A. Madulid, Mount Bloomfield, Palawan, Philippines: the scrub and *gymnostoma*-woodland, in *Proceedings of the Second International Conference on Serpentine Ecology*, edited by T. Jaffré, pp. 21–29, Orstom, Noumea, New Caladonia, 1997.

Proctor, J., A. J. M. Baker, M. M. J. van Balgooy, L. A. Bruijnzeel, S. H. Jones, and D. A. Madulid, Mount Bloomfield, Palawan, Philippines: forest on greywacke and serpentinized peridotite, *Edinburgh Journal of Botany*, *56*, In press., 2000a.

Proctor, J., L. A. Bruijnzeel, and A. J. M. Baker, What causes the vegetation types on Mount Bloomfield, a coastal tropical mountain of the western Philippines?, *Global Ecology and Biogeography Research Letter*, *8*, In press., 2000b.

Raich, J. W., and W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus*, *44B*, 81–99, 1992.

Rauland-Rasmussen, K., Aluminium contamination and other changes of acid soil solution insolated by means of porcelain suction-cups, *Journal of Soil Science*, *40*, 95–101, 1989.

Reich, P. B., M. B. Walters, and D. S. Ellsworth, Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species, *Oecologia*, *86*, 16–24, 1991.

Richards, B. N., J. E. N. Smith, G. L. White, and J. L. Charley, Mineralization of soil nitrogen in three forest communities from the New England region of New South Wales, *Australian Journal of Ecology*, *10*, 429–441, 1985.

Richards, L. A., Capillary conduction of liquids through porous mediums, *Physics*, *1*, 318–333, 1931.

Richards, P. W., *The tropical rain forest*, Cambridge University Press, Cambridge, U. K., 1952.

Richardson, J. H., Some implications of tropical forest replacement in Jamaica, *Z. Geomorph. N.F.*, *44*, 107–118, 1982.

Roberts, J. M., R. Hopkins, and M. Morecroft, Towards a predictive description of forest canopies from litter properties, *Functional Ecology*, *13*, 265–272, 1999.

Robertson, G. P., and P. M. Vitousek, Nitrification potentials in primary and secondary succession, *Ecology*, *62*, 376–386, 1981.

Roche, M. A., Evapotranspiration réelle de la forêt amazonienne en Guyane, *Cahiers de l'ORSTOM, Séries Hydrologie*, *19*, 37–44, 1982.

Rodda, The rainfall measurement problem, *International Association of Hydrological Scientific Publications*, *75*, 215–231, 1967.

Ross, J., Radiative transfer in plant communities, in *Vegetation and the atmosphere*, edited by J. L. Monteith, vol. 1, pp. 13–15, Academic Press, London, U. K., 1975.

Rost-Siebert, K., Untersuchungen zur H- und Al-Ionentoxizität an Keimpflanzen von Fichte (*Picea abies*, Karst.) und Buche (*Fagus silvatica*, L.) in lösungskultur, *Berichte des Forschungszentrums Waldökosysteme/Waldsterben Reihe A, Bd. 12*, Universität Göttingen, Göttingen, Germany, 1985.

Rout, S. K., and S. R. Gupta, Soil respiration in relation to abiotic factors, forest floor litter, root biomass and litter quality in forest ecosystems of Siwaliks in northern India, *Acta Ecologia Ecol. Plant.*, *10*, 224–244, 1989.

Roy, A. K., A. Sharma, and G. Talukder, Some aspects of aluminum toxicity in plants, *The Botanical Review*, *54*, 145–178, 1988.

Russell, S., Measurement of mist precipitation, *Techniques notebook, The Bryological Times*, 1984.

Rutter, A. J., An analysis of evaporation from a stand of Scots pine, in *International Symposium on Forest Hydrology*, edited by W. E. Sopper and H. W. Lull, pp. 403–417, Pergamon Press, Oxford, UK, 1967.

Rutter, A. J., The hydrological cycle in vegetation, in *Vegetation and the atmosphere. Vol. 1. Principles*, edited by J. L. Monteith, chap. 4, pp. 111–154, Academic Press, London, 1975.

Sachs, L., *Statistische Methoden. Ein Soforthelfer*, Springer-Verlag, Berlin, 1970.

Sanchez, P. A., *Properties and management of soils in the tropics*, John Wiley & Sons, New York, 1976.

Santiago, L. S., G. Goldstein, F. C. Meinzer, J. H. Fownes, and D. Mueller-Dombois, Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest, *Tree Physiology*, *(In press)*, 1999.

Scatena, F. N., W. Silver, T. Siccama, A. Johnson, and M. J. Sánchez, Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Purto Rico, before and after Hurricane Hugo, 1989, *Biotropica*, *25*, 5–27, 1993.

Scatena, F. N., S. Moya, C. Estrada, and J. D. Chinea, The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, *Biotropica*, *28*, 424–440, 1996.

Schellekens, J., VAMPS, a Vegetation -AtMospheric -Plant -Soil water flow model, *Internal report*, Vrije Universiteit, Amsterdam, the Netherlands, 1996.

Schellekens, J., L. A. Bruijnzeel, A. J. Wickel, F. N. Scatena, and W. L. Silver, Interception of horizontal precipitation by elfin cloud forest in the Luquillo Mountains, Eastern Puerto Rico, in *First International Conference on Fog and Fog Collection*, edited by R. S. Schemenauer and H. Bridgman, pp. 29–32, Vancouver, 1998.

Schellekens, J., L. A. Bruijnzeel, F. N. Scatena, F. Holwerda, and N. J. Bink, Evaporation from a tropical rain forest, Luquillo Experimental Forest, eastern Puerto Rico, *Water Resources Research*, *In press*, 2000.

Schemenauer, R. S., and P. Cereceda, A proposed standard fog collector for use in high-elevation regions, *Journal of Applied Meteorology*, *33*, 1313–1322, 1994.

Schier, G. A., and K. F. Jensen, Atmospheric deposition effects on foliar injury and foliar leaching in red spruce, in *Ecology and decline of red spruce in the eastern United States*, edited by C. Eagar and M. B. Adams, vol. 96 of *Ecological Studies*, pp. 271–294, Springer-Verlag, Berlin, Germany, 1992.

Schlesinger, W. H., Carbon balance in terrestrial detritus, *Annual Review of Ecology and Systematics*, *8*, 51–81, 1977.

Schröter, C., *Das Pflanzenleben der Alpen*, Albert Raustein, Zurich, Swiss, 1926.

Scott, D. A., J. Proctor, and J. Thompson, Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil. II. Litter and nutrient cycling, *Journal of Ecology*, *80*, 705–717, 1992.

Shreve, F., *A montane rain forest: a contribution to the physiological plant geography of Jamaica*, Carnegie Institution, Washington, U. S., 1914.

Shuttleworth, W. J., Evaporation from Amazonian rainforest, *Philosophical Transactions of the Royal Society*, *B233*, 321–346, 1988.

Silver, W. L., and K. A. Vogt, Fine root dynamics following single and multiple disturbance in a subtropical wet forest ecosystem, *Journal of Ecology*, *81*, 729–738, 1993.

Silver, W. L., F. N. Scatena, A. H. Johnson, T. G. Siccama, and M. J. Sanchez, Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations, *Plant and Soil*, *164*, 129–145, 1994.

Silver, W. L., A. E. Lugo, and M. Keller, Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils, *Biogeochemistry*, *44*, 301–328, 1999.

Simon, B., and G. M. Rothe, Aluminiumbedingte Stoffwechselanderungen in Fichtenkeimlingen, *Algemeine Forst- and Jagdzeitung*, *36*, 931–935, 1985.

Singh, J. S., and S. R. Gupta, Plant decomposition and soil respiration in terrestrial ecosystems, *Botanical Review*, *43*, 449–528, 1977.

Smit, E., Destruction by micro-wave oven CEM MDS-81D, *Standard operating procedure no. w 0020*, Department of Ecology and Ecotoxicology, Vrije Universiteit, Amsterdam, the Netherlands, 1995.

Sokal, R. R., and F. J. Rohlf, *Biometry*, Freeman, San Fransisco, 1981.

Songwe, N. C., F. E. Fasehuna, and D. U. Okali, Litterfall and productivity in a tropical rain forest, Southern Bakundu Forest Reserve, Cameroon, *Journal of Tropical Ecology*, *4*, 25–37, 1988.

Sørensen, L. H., Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated addition of organic matter, *Soil Biology and Biochemistry*, *6*, 287–392, 1974.

Spain, A. V., Litterfall and the standing crop of litter in three tropical Australian rainforest, *Journal of Ecology*, *72*, 947–961, 1984.

Sparks, J. P., and J. R. Ehleringer, Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects, *Oecologia*, *109*, 362–367, 1997.

Spiegel, M. R., *Theory and Problems of Statistics*, Schaum's Outline Series, McGraw-Hill Book Company, London, UK, 1972.

Spijkerman, L., *Comparison of four mountainous forest soils, Blue Mountains, Jamaica*, Msc. thesis, Universiteit van Amsterdam, Amsterdam, The Netherlands, 1996.

Stadtmüller, T., and N. Agudelo, Amount and variability of cloud moisture input in a tropical cloud forest, *International Association of Hydrological Sciences Publication*, *193*, 25–32, 1990.

Stadtmüller, T., *Cloud forests in the humid tropics: a bibliographic review*, The United Nations University, Tokyo and Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica, 1987.

Stakman, W. P., Measuring soil moisture, *I.L.R.I. Publications 16*, International institute for Land Reclamation and Improvement, Wageningen, The Netherlands, 1973.

Steinhardt, U., Untersuchungen über den Wasser- und Nährstoffhaushalt eines Andinen Wolkenwaldes in Venezuela, *Göttinger Bodenkundliche Berichte 56*, Institut für Bodenkunde und Waldernährung, Göttingen, Germany, 1979.

Steinhardt, U., and H. W. Fassbender, Caracterïisticas y composición quïmica de las Iluvas de los Andes occidentales de venezuela, *Turrialba*, *29*, 175–182, 1979.

Stewart, C. G., Fine root growth in response to local nutrient enrichment in two tropical montane forests, *Biotropica*, *Submitted*, 1999.

Stewart, J. B., Evaporation from the wet canopy of a pine forest, *Water Resources Research*, *13*, 915–921, 1977.

Stoorvogel, J. J., *Gross inputs and outputs of nutrients in undisturbed forest, Taï Area, Côte d'Ivoire*, vol. 5 of *Tropenbos Series*, The Tropenbos Foundation, Wageningen, The Netherlands, 1993.

Sugden, A. M., The montane vegetation and flora of Margarita Island, Venezuela, *Journal of Ecology*, *69*, 263–275, 1986.

Swift, M. J., O. W. Heal, and J. M. Anderson, *Decomposition in terrestrial ecosystems*, vol. 5, Blackwell Scientific Publications, Oxford, 1979.

Sylvia, D. M., J. Fuhrmann, P. G. Hartel, and D. A. Zuberer, *Principles and applications of soil microbiology*, Prentice-Hall, New Jersey, U. S. A., 1998.

Tamm, C. O., *Nitrogen in terrestrial ecosystems*, vol. 81 of *Ecological Studies*, Springer-Verlag, Berlin, Germany, 1991.

Tanner, E. V. J., Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations, *Journal of Ecology*, *65*, 883–918, 1977a.

Tanner, E. V. J., *Mineral cycling in montane forests in Jamaica*, Ph.D. thesis, University of Cambridge, Cambridge, U. K., 1977b.

Tanner, E. V. J., Litterfall in montane rain forests in Jamaica and its relation to climate, *Journal of Ecology*, *68*, 883–848, 1980a.

Tanner, E. V. J., Studies on the biomass and productivity in a series of montane rain forests in Jamaica, *Journal of Ecology*, *68*, 573–588, 1980b.

Tanner, E. V. J., The decomposition of leaf litter in Jamaican montane rain forests, *Journal of Ecology*, *69*, 263–275, 1981.

Tanner, E. V. J., Jamaican montane forests: nutrient capital and cost of growth, *Journal of Ecology*, *73*, 553–568, 1985.

Tanner, E. V. J., and V. Kapos, Leaf structure of Jamaican upper montane rain forest trees, *Biotropica*, *14*, 16–24, 1982.

Tanner, E. V. J., V. Kapos, S. Freskos, J. R. Healey, and A. M. Theobald, Nitrogen and phosphorus fertilization of Jamaican montane forest trees, *Journal of Tropical Ecology*, *6*, 231–238, 1990.

Tanner, E. V. J., P. M. Vitousek, and E. Cuevas, Experimental investigation of nutrient limitation of forest growth on wet tropical mountains, *Ecology*, *79*, 10–22, 1998.

Tate, K. R., D. J. Ross, B. J. O'Brien, and F. M. Kelliher, Carbon storage and turnover, and respiration activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest, *Soil Biology and Biochemistry*, *25*, 1601–1612, 1993.

Taylor, G. J., and C. D. Foy, Mechanisms of aluminium tolerance in *Triticum aestivum* L. (wheat). IV. The role of ammonium and nitrate nutrition, *Canadian Journal of Botany*, *63*, 2181–2186, 1985.

Teuben, A., and T. A. P. J. Roelofsma, Dynamic interactions between functional groups of soil arthropods and micro-organisms during decomposition of coniferous litter in microcosm experiments, *Biology and Fertility of Soils*, *9*, 145–151, 1990.

Thalman, A., Zur Methodik der Bestimmung der Hydrogenaseactivitat in Bodem mittels Triphenyltetrazoliumchlorid (TTC), *Landwirtschaftliche Forschungen*, *21*, 249–258, 1968.

Thom, A. S., Momentum, mass and heat exchange of plant communities, in *Vegetation and the atmosphere. Vol. 1. Principles*, edited by J. L. Monteith, pp. 57–109, Academic Press, London, 1975.

Thomas, G. W., Exchangeable cations, in *Chemical and microbiological properties*, vol. part 2 of *Methods of soil analysis*, pp. 159–165, American Society of Agronomy, Madison, Wisconsin, U. S., 1982.

Tillman, J. E., The indirect determination of stability, heat and momentum fluxes in the atmosphere boundary layer from simple scalar variables during dry unstable conditions, *Journal of Applied Meteorology*, *11*, 783–792, 1972.

Tischner, R., R. Kaiser, and Hüttermann, Untersuchungen zum Einfluß von Aluminium-Ionen auf das Wachstum von Fichten-keimlingen in Abhängigkeit von pH-Wert, *Forstw. Cbl.*, *102*, 329–335, 1983.

Troll, C., Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- and Südhalbkugel, *Ber. geobot. ForschInst. Rüel*, *1947*, 46–83, 1948.

Tukey, H. B., Leaching of metabolites from foliage and its implication in the tropical rain forest, in *A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico*, edited by H. Odum and R. Pidgeon, pp. H155–H160, U.S. Atomic Energy Commission, Oak Ridge, Tennessee, U. S., 1970.

Turton, S. M., Light environments within montane tropical rainforest, Mt Bellenden Ker, North Queensland, *Australian Journal of Ecology*, *15*, 35–42, 1990.

Van Genuchten, M. T., A closed form equation for predicting the hydraulic conductivity of unsaturated soils, *Soil Science Society of America Journal*, *44*, 892–898, 1980.

Van Steenis, C. G. G. J., An attempt towards an explanation of the effect of mountain mass elevation, *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, *64*, 435–442, 1961.

Van Steenis, C. G. G. J., *The mountain flora of Java*, Brill, Leiden, 1972.

Van Straalen, N. M., and P. C. Rijninks, The efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod population, *Pedobiologia*, *24*, 197–209, 1982.

Van Veen, J. A., and E. A. Paul, Conversion of biovolume measurements of soil organisms, grown under various moisture tensions, to biomass and their nutrient content, *Applied Environmental Microbiology*, *37*, 686–692, 1979.

Vance, E., and N. M. Nadkarni, Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest, *Soil Biology and Biochemistry*, *22*, 677–684, 1990.

Vaughan, D., and B. Ord, Influence of polyphenolic acids on morphological changes in roots of *Pisum sativum*, *Journal of the Science of Food and Agriculture*, *52*, 289–299, 1990.

Veneklaas, E. J., *Rainfall interception and aboveground nutrient fluxes in Colombian montane tropical rain forests*, Ph.D. thesis, Rijksuniversiteit Utrecht, Utrecht, The Netherlands, 1990.

Veneklaas, E. J., and R. Van Ek, Rainfall interception in two tropical montane rain forests, Columbia, *Hydrological Processes*, *4*, 311–326, 1990.

Verhoef, H. A., and L. Brussaard, Decomposition and nitrogen mineralization in natural and agro-ecosystems: the contribution of soil fauna, *Biogeochemistry*, *11*, 175–211, 1990.

Vitousek, P. M., Litterfall, nutrient cycling, and nutrient limitation in tropical forests, *Ecology*, *65*, 285–298, 1984.

Vitousek, P. M., and R. L. Sanford, Nutrient cycling in moist tropical forest, *Annual Reviews of Ecological Systems*, *17*, 137–167, 1986.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, and W. A. Reiners, A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems, *Ecological Monographs*, *52*, 155–177, 1982.

Vitousek, P. M., K. Van Cleve, N. Balakrishnan, and D. Mueller-Dombois, Soil development and nitrogen turnover in montane rainforest soils in Hawai'i, *Biotropica*, *15*, 268–274, 1983.

Vitousek, P. M., P. A. Matson, and D. R. Turner, Elevational and age gradients on Hawaiian montane rainforests: foliar and soil nutrients, *Oecologia*, *77*, 565–570, 1988.

Vitousek, P. M., C. B. Field, and P. A. Matson, Variation in foliar $\delta^{13}C$ in Hawaiian *Metrosideros polymorpha*: a case of internal resistance?, *Oecologia*, *84*, 362–370, 1990.

Vitousek, P. M., G. Aplet, D. Turner, and J. J. Lockwood, The Mauna Loa environmental matrix: foliar and soil nutrients, *Oecologia*, *89*, 372–382, 1992.

Vossbrinck, C. R., D. C. Coleman, and T. A. Wooley, Abiotic and biotic factors in litter decomposition in a semiarid grassland, *Ecology*, *60*, 265–271, 1979.

Vugts, H. F., M. J. Waterloo, F. J. Beekman, K. F. A. Frumau, and L. A. Bruijnzeel, The temperature variance method: a powerful tool in the estimation of actual evaporation rates., in *Hydrology of Warm Humid Regions*, edited by J. S. Gladwell, IAHS Publication no. 261, pp. 251–260, 1993.

Wadsworth, F. H., and J. A. Bonnet, Soil as a factor in the occurrence of two types of montane forest in Puerto Rico, *Caribbean Forester*, *12*, 67–70, 1951.

Wallwork, J. A., *Ecology of soil animals*, McGraw-Hill, London, U.K., 1970.

Walmsley, J. L., W. R. Burrows, and R. S. Schemenauer, The use of routine weather observations to calculate liquid water content in summertime high-elevation fog, *Journal of Applied Meteorology, (In press)*, 1999.

Ward, R. C., and M. Robinson, *Principles of Hydrology*, McGraw-Hill, Maidenhead, UK, 1990.

Warner, H., Soil respiration, litter fall and productivity of tropical rain forest, *Journal of Ecology, 58*, 543–547, 1970.

Waterloo, M. J., *A hydrological study of the mass elevation effect on Gunung Silam, a small coastal ultrabasic mountain in Sabah, East Malaysia*, Msc. thesis, Vrije Universiteit, Amsterdam, the Netherlands, 1989.

Waterloo, M. J., L. A. Bruijnzeel, H. F. Vugts, and T. T. Rawaqa, Evaporation from *Pinus caribaea* plantations on former grassland soils under maritime tropical conditions, *Water Resources Research, 35*, 2133–2144, 1999.

Waterman, P. G., and S. Mole, *Methods in ecology: analysis of phenolic plant metabolites*, Blackwell Scientific Press, Oxford, 1994.

Weaver, P. L., Cloud moisture interception in the Luquillo Mountains of Puerto Rico, *Caribbean Journal of Science, 12*, 129–144, 1972.

Weaver, P. L., M. D. Byer, and D. Bruck, Transpiration rates in the Luquillo Mountains of Puerto Rico, *Biotropica, 5*, 123–133, 1973.

Weaver, P. L., E. Medina, D. Pool, K. Dugger, J. Gonzales-Liboy, and E. Cuevas, Ecological observations in the dwarf cloud forest of the Luquillo Mountains of Puerto Rico, *Biotropica, 18*, 79–85, 1986.

Werner, W. L., Canopy dieback in the upper montane rain forests of Sri Lanka, *GeoJournal, 17*, 245–248, 1988.

Whipps, J. M., and J. M. Lynch, The influence of the rhizosphere on crop productivity, *Advances in Microbial Ecology, 6*, 187–244, 1986.

Whitehead, H. C., and J. H. Feth, Chemical composition of rain, dry fallout and bulk precipitation at Menlo Park, California, 1957–1959, *J. Geophys. Res., 69*, 3319–3333, 1964.

Whitmore, T. C., *An introduction to tropical rain forest*, 2nd ed., Clarendon Press, Oxford, 1998.

Whitmore, T. C. W., Tropical forest nutrients, where do we stand? a tour de horizon, in *Mineral nutrients in tropical forest and savanna ecosystems*, edited by P. J, pp. 1–13, Blackwell Scientific Press, Oxford, 1989.

Williams, D. G., and J. R. Ehleringer, Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient, *Oecologia*, *106*, 455–460, 1996.

Zadroga, F., The hydrological importance of a montane cloud forest area of Costa Rica, in *Tropical agricultural hydrology*, edited by R. Lal and E. W. Russell, pp. 59–73, John Wiley & Sons, New York, 1981.

Ziska, L. H., A. H. Teramura, and J. H. Sullivan, Physiological sensitivity of plants along an elevational gradient to UV-B radiation, *Australian Journal of Botany*, *79*, 863–871, 1992.

Zotz, G., and K. Winter, Short-term photosynthesis measurements predict leaf carbon balance in tropical rain-forest canopy plants, *Planta*, *191*, 409–412, 1993.

A

DESCRIPTION OF SOIL PROFILES

A.1 WELL-DEVELOPED MULL RIDGE FOREST

Soil type: Dystric cambisol [*FAO-UNESCO*, 1990]
Pit located on a level ridge section at *c.* 1600 *m* a.s.l., adjacent to sites of *Tanner* [1980b]; few seedlings on forest floor; no signs of (saturated) overland flow; (moderately) well-drained.

L [+6–+4 *cm*] Thin and discontinuous litter layer; litter can be abundant after leaf shedding by *Clethra occidentalis* (January–February; Chapter 8))

F+H [+4–0 *cm*] brownish black organic horizon, well fragmented, loose/powdery material; no aggregates; abundant very fine roots, increasingly coarse with depth; *Mycorrhizae* present, no visible fungi; abundant microfauna; smooth and abrupt transition to

Ah [0–14 *cm*] dull yellowish brown (10 YR 5/3) sub-angular blocky silty loam; friable to firm; non-sticky; moderate to medium roots ($\leq$5 *mm*); few macro-pores; gradual and slightly wavy transition to

Bh [14–30 *cm*] yellowish brown (10 YR 5/6) sub-angular blocky clay loam of low friability; slightly sticky; few fine root (<3 *mm*), decomposed (very fine) roots present throughout horizon; abrupt and smooth boundary to

B1 [30–54 *cm*] (bright) yellowish brown (10 YR, 5/6–6/6) sub-angular blocky sandy clay; firm; very sticky, plastic; very few living roots; wavy and thin transition to
[54–56 *cm*] bright reddish brown (2.5 YR 5/6) sub-angular blocky sandy clay (oxidation layer?); very firm, very sticky; sometimes interrupted; wavy and thin transition to

B2 [56–89 *cm*] yellowish brown (10 YR 5/8) sub-angular blocky compact clay; very firm, very sticky; very few very fine roots (<1 *mm*); former root channels create macro-pores; at 85 *cm* a thin, irregular and broken layer of reduced grey clay with common red mottles; sometimes signs of oxidation above this thin layer; irregular transition to

B3 [>89 *cm*] bright yellowish brown (10YR 6/6); sub-angular blocky compact clay; very sticky, very plastic, very few roots.

A.2 POORLY-DEVELOPED MULL FORESTS PROFILE

Soil type: *Dystric cambisol* [*FAO-UNESCO*, 1990]
Pit located on a relatively flat area of the NNW sloping ridge side just outside the plot boundary at 1809 *m* a.s.l.; relatively dense understorey of ferns and Jamaican bamboo (*Chusquea abietifolia*).

L [+6–+4 *cm*] Thin and discontinuous litter layer, numerous fallen and decomposing trunks covered with moss

F+H [+4–0 *cm*] black (7.5 YR 2/1, top) to brown/greyish brown (7.5 YR 4/2, bottom) small, incomplete granules; no layered structure at top, semi-layered moder at bottom; abundant very fine/fine hairy and nodulated roots (>50 % of volume) growing in decomposed leaves; 20 % of roots have abundant *Mychorrizae*, no visible fungi; abundant macro-pores

T [0–1 *cm*] thin transition zone between organic- and mineral horizons; greyish brown (7.5 YR 4/2) well-rounded granular organic material with mineral sub-angular blocky fine silt; very friable, slightly sticky; frequent micro- and macro-pores; wavy transition to

Ah [1–14 *cm*] dark brown (10 YR 3/3) fine granular to sub-angular blocky loam; friable, very slightly sticky; common very fine roots (<0.5 *mm*); many very fine to medium pores; abrupt and wavy boundary to

Bh [14–38 *cm*] brown (10 YR 4/4) granular to sub-angular blocky silty loam; texture increasingly loamy with depth; slightly sticky, friable; common fine to coarse roots; many fine pores, pore size increase with depth; abrupt and smooth boundary to

Bw1 [38–65 *cm*] brown (10 YR 4/4) fine to medium sub-angular blocky loamy silt with common grey (5 Y 5/1) weathered particles of parent material ($\leq$1 *cm*); structure becomes more massive with depth; slightly sticky, friable (top) to firm (bottom); common fine to very fine pores; very few fine roots; vague, wavy boundary to

Bw2 [65–82 *cm*] brown (10 YR 4/4 at the top) to reddish brown (2.5 YR 4/6) medium to coarse angular blocky loam; increasing amounts of medium to coarse rotten rock with depth; friable; non-sticky, increasingly heavy with depth; common very fine pores; single large root at 68 *cm*; vague transition to

C [>82 *cm*] red (10 R 4/6) half weathered andesitic rotten rock, grading to fresh andesitic bed rock at unknown depth.

A.3 Moderately-developed Mor forest profile

Soil type: Folic histosol [*FAO-UNESCO*, 1990]

Pit located at northern edge of ridge on gently sloping northerly slope at 1824 *m* a.s.l.; litter layer is thick ($\geq$ 5 *cm*); no possibility for overland flow; dense understorey of ferns.

L [+30–+27 *cm*] Litter, sometimes overgrown with moss; *Elaphoglossum latifolium* is common, few bromeliads, few decomposing trunks.

F [+27–+22 *cm*] Irregularly fermented material, fragmented and inter-twined with abundant very fine roots, moderately hairy; root mat has spongy structure; leaf fragments identifiable throughout horizon; *Mychorrizae* locally abundant, no visible fungi; clear, wavy but clear boundary to H horizon, characterized by abrupt, strong increase in coarse roots with depth

H [+22–0 *cm*] black (10 YR 1.7/1) to dark brown fine well-rounded, non-sticky aggregates, very friable, very light (fluffy) humus; abundant very fine roots, decreasing and coarser in bottom half (diameter >10 *mm*); very few *Mychorrizae*; no visible fungi; abundant macro-pores; abrupt, smooth but wavy transition to

Ah [0–5 *cm*] very dark brown (7.5 YR 2/3) highly organic silty loam with well-rounded granules with a loose structure and mineral nucleus; very friable when wet; illuviation from H horizon evident; few very fine roots, very few coarse roots; no visible *Mychorrizae*, no visible fungi; abundant macro-pores; sharp and smooth transition to

Bh [5–10 *cm*] dull yellowish brown (10 YR 4/3) silt with very small granules; loose fine to medium crumb; sticky, very friable; structure is complete (aggregates are separated); medium to few roots; frequent fine to coarse pores; very few pieces of rotten rock; abrupt and smooth boundary to

Bw [10–35 *cm*] dull yellowish brown (10 YR 4/3 at the top) to brown (10 YR 4/4 at the bottom) loamy silt matrix with sub-angular, irregularly weathered rotten rock in a lenticular setting; matrix sticky and increasingly friable with depth; non-weathered angular large stones (diameter >10 *cm*) at shallow depths (<25 *cm*); very few roots; many fine to medium pores; abrupt smooth boundary to

BC/C [>35 *cm*] brown (10 YR 4/4–4/5) coarse sandy loam matrix with increasing amounts of weathered andesitic lava; fine to medium sub-angular blocky; slightly sticky, friable; many fine to medium pores.

A.4 Mor Ridge forest profile

Folic histosol [*FAO-UNESCO*, 1990]

Pit situated on the north side of the ridge on a moderately sloping (15°) NNE slope at *c.* 1600 *m* a.s.l.; abundant *Elaphoglossum latifolium*, bromeliads and mosses (*Leucobryum gigantum*); no possibility for (saturated) overland.

L [+50/37 *cm*–+35/28 *cm*] Litter layer, overgrown with *E. latifolium* and terrestrial bromeliads.

F [+35/28–+14 *cm*] brownish black (7.5YR 2/2) fragmented litter, fermentation irregularly distributed; leaf fragments identifiable throughout the horizon; some fungi present, inter-twined with abundant very fine to fine roots; abundant root hairs, no visible *Mycorrhizae*; firm root mat with platy structure; material is loose; clear transition to H, wavy outline not always recognizable, characteristic transition from abundant fine roots to coarse roots

H [+14–0 *cm*] granular aggregates up to 2 *cm* (incomplete in upper part); increasing aggregate size and firmness with depth; abundant fine to very fine roots; abundant macro-pores; few fungi; no visible *Mycorrhizae*; abrupt and smooth transition to

Ah [0–9 *cm*] brownish black (7.5 YR, 3/2) clay loam; decreasing aggregate size (2 *cm*–1 *mm*) with depth, structure in lower parts complete; aggregates sticky and plastic; few very fine roots, fine roots present, few coarse roots; fungi present; macro-pores decreasing with depth

Bhw [9–19 *cm*] brownish black (10YR, 3/2) sub-angular, loose structured, silty loam; greyish red/yellow sub-angular blocky stones (≤5 *cm*) throughout horizon; some woody roots (≤4 *mm*), no very fine roots; clear transition (but with irregular outline) to

Bw [19–39/54 *cm*] spotted colour patterns: brown (7.5 YR, 4/3–4/4), greyish brown (7.5 YR, 5/2) and dull reddish brown / brownish grey (5 YR, 5/3–5/1); small sub-angular blocky, gravely clay loam with increased amounts of weathered stones (>50 % of bulk); very few roots; abundant brown/redish brown coated macro-pores; clear, irregular but gradual transition to

BC [54–70 *cm*] purplish grey (5 RP, 5/1) brown gravely, sandy clay loam with predominantly small stones

C [>70 *cm*] purplish grey (5 RP, 5/1) brown heavily weathered andesitic lava.

B

TEMPERATURE VARIANCE METHOD

Under dry unstable atmospheric conditions H (Eq. 5.7 on page 107) can be related to near-surface turbulent fluctuations in air temperature, the intensity of which is described by the standard deviation (σ_T) of high-frequency measurements of the air temperature T (K) according to [*Tillman*, 1972; *De Bruin*, 1982]:

$$H = \rho C_p \left[(\frac{\sigma_T}{C_1})^3 (g\,k\,\frac{z}{T}) \frac{(1 - C_2\,\zeta)}{-\zeta} \right]^{\frac{1}{2}} \tag{B.1}$$

where:

ρ	dry air density	$[kg\,m^{-3}]$
C_p	specific heat of air at constant temperature T	$[J\,kg^{-1}\,K^{-1}]$
σ_T	standard deviation of temperature fluctuations	$[K]$
g	acceleration term of gravity	$[m\,s^{-1}]$
z	observation height above the ground surface	$[m]$
T	air temperature	$[K]$
ζ	stability parameter	[-]
k	von Kármán's constant, 0.41	[-]
C_1, C_2	empirical constants (2.9, 28.4; *De Bruin* [1982])	[-]

According to the Monin-Obukhov theory the stability term ζ equals:

$$\zeta = \frac{z - d}{L} \tag{B.2}$$

where L is the 'Obukhov stability length', a length scale connected to the production (or destruction) of turbulent kinetic energy by buoyancy. L is defined by:

$$L = \frac{-u_*^3\,\rho\,T\,C_p}{k\,g\,H} \tag{B.3}$$

for which the friction velocity u_* can be evaluated using the logarithmic wind profile equation:

$$u_* = \frac{u(z) \cdot k}{ln\,(\frac{z-d}{z_0})} \tag{B.4}$$

Equations B.1, B.2, and B.3 can be solved by iteration (generally $n = 3$–5) until constant estimates for H (differences $<0.001\ Wm^{-2}$) are obtained.

In case of unstable atmospheric conditions and free convection, ζ equals the Richardson number (Ri) and becomes < -0.1, which allows the simplifi- on

of Eq. B.1 to:

$$H = 1.075 \cdot \rho\, C_p\, \sigma_T{}^{\frac{3}{2}} \left(\frac{g\, k\, z}{T}\right)^{\frac{1}{2}} \tag{B.5}$$

For observations made above a vegetated surface it is necessary to replace z in Eqs. B.1 and B.5 by $z - d$ where d is the zero-plane displacement height (in m). The TVAR method is valid under unstable atmospheric conditions only (*i.e.* $Ri < -0.1$). Computations of H and λE using Eq. B.5 were therefore restricted to daytime observations as indicated by $R_n > 100\ W m^{-2}$ (generally between 08:00 and 16:00 h) and wind speeds at 5.9 m below 1.9 $m\, s^{-1}$. For $u_{5.9m} \geq 1.9$ $m\, s^{-1}$ (but with the same restriction on R_n) Eq. B.1 was used. Nighttime transpiration was assumed negligible. In addition, half-hourly records within a period from 2 h prior- to 2 h after any precipitation event >0.44 mm were excluded to ensure conditions with a fully dried canopy.

C

DESCRIPTION OF THE SVAT MODEL VAMPS

Daily values of drainage D and changes in soil water storage ΔS in the two forest plots were evaluated using the one-dimensional Soil-Vegetation-Atmosphere-Transfer (SVAT) model VAMPS [*Schellekens*, 1996]. VAMPS consist of three modules describing throughfall (net precipitation), transpiration and soil water fluxes through forested areas that can be combined or used separately. The present applications were limited to soil water dynamics as daily values of net precipitation (throughfall plus stemflow) and transpiration were determined independently of the model.

The soil water module of VAMPS was adapted from the soil water simulation model SWATR* [*Feddes et al.*, 1978]. Water fluxes in the unsaturated zone are calculated by solving an adapted ψ_m-based form of the numerical solution of the basic Richards equation for unsteady unsaturated flow as described by *Feddes et al.* [1978] and *Belmans et al.* [1983]. A differential moisture capacity term ($C(h)$) was introduced as a single independent variable equal to the slope of the soil-moisture retention curve, $d\theta/d\psi_m$:

$$\frac{\partial \psi_m}{\partial t} = \frac{1}{C(\psi_m)} \frac{\partial}{\partial z} \left[K(\psi_m)(\frac{\partial \psi_m}{\partial z} - 1) \right] \tag{C.1}$$

In addition, a sink term (S) is used to accommodate water extraction by roots per unit bulk volume of soil per unit time ($cm^3\, cm^{-3}\, d^{-1}$):

$$\frac{\partial \psi_m}{\partial t} = \frac{1}{C(\psi_m)} \frac{\partial}{\partial z} \left[K(\psi_m)(\frac{\partial \psi_m}{\partial z} - 1) \right] - \frac{S(\psi_m)}{C(\psi_m)} \tag{C.2}$$

where:

ψ_m	soil water pressure head	$[cm]$
t	time	[days]
C	differential water capacity ($d\theta/d\psi_m$)	$[cm^{-1}]$
S	sink term	$[cm^3\, cm^{-3}\, d^{-1}]$
z	height (taken positive upwards)	$[cm]$

*The SWAP/SWATR models are maintained and documented by the Department of Agrohydrology, Winand Staring Centre, Wageningen, the Netherlands.

VAMPS can handle several boundary conditions at the bottom of the selected soil profile; free drainage at the profile bottom (taken here at 80 *cm* depth) was assumed in this study. The relations between soil water content θ, pressure head ψ_m and the unsaturated conductivity $K(\theta)$ in VAMPS are described using the so-called Van Genuchten equations [*Van Genuchten*, 1980] in which the dimensionless water content θ is given as:

$$\theta = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha\,\psi_m)^n]^m} \tag{C.3}$$

where:

θ	actual soil water content
θ_s	saturated soil water content ($\psi_m = 0$)
θ_r	residual soil water content (normally taken at $\psi_m = -1.58\ MPa$)
α, n	soil specific parameters describing the ψ_m - θ relationship
m	related to n by $1 - \frac{1}{n}$

Furthermore:

$$K(\psi_m)_{relative} = \frac{\left[1 - (\alpha\,\psi_m)^{n-1} \cdot [1 + (\alpha\,\psi_m)^n]^{-m}\right]^2}{[1 + (\alpha\,\psi_m)^n]^{\frac{m}{2}}} \tag{C.4}$$

where:

$$K(\psi_m)_{relative} = \frac{K(\psi_m)}{K_{sat}} \tag{C.5}$$

The values of α, n and m were obtained by non-linear regression analysis [*Marquardt*, 1963] using measured ψ_m - θ curves.